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STUDIES IN ROOT-PARASITISM

THE HAUSTORIUM OF SANTALUM ALBUM

Part 2.—The Structure of the Mature Haustorium and the Inter-relations between Host and Parasite

BY

C. A. BARBER, M.A., F.L.S

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CONTENTS.

Vol. I.

		Pages.
No. I.	Barber, C. A. Studies in Root-Parasitism. The Haustorium of Santalum Album—	
	Part I. Early Stages. (With seven plates) ...	30
	„ II. The Structure of the Mature Haustorium and the Inter-relations between Host and Parasite. (With sixteen plates) ...	58
No. II.	Butler, E. J., and Hayman, J. M. Indian Wheat Rusts, with a Note on "The Relation of Weather to Rust on Cereals" by W. H. Moreland. (With five plates)...	57
No. III.	Butler, E. J. Fungus Diseases of Sugarcane in Bengal. (With eleven plates)	53
No. IV.	Burkill, I. H. *Gossypium obtusifolium*, Roxburgh. (With one plate)	10
No. V.	Butler, E. J. An Account of the Genus Pythium and some Chytridiaceæ. (With ten plates)	158
No. VI.	Mann, Harold H., and Hutchinson, C. M. *Cephaleuros virescens*, Kunze. The Red Rust of Tea. (With eight plates)	33

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AUGUST, 1907. BOTANICAL SERIES. VOL. I, NO. 1, PART II.

MEMOIRS OF THE DEPARTMENT OF AGRICULTURE IN INDIA.

STUDIES IN ROOT-PARASITISM.

THE HAUSTORIUM OF SANTALUM ALBUM.

PART 2.—THE STRUCTURE OF THE MATURE HAUSTORIUM AND THE INTER-RELATIONS BETWEEN HOST AND PARASITE.

BY

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TABLE OF CONTENTS.

FIRST PAPER.

(Memoirs of the Department of Agriculture in India, Botanical Series, Vol. I, No. 1.)

1. Introduction: the haustoria on the roots of *Santalum, Cansjera, Olax Ximenia, Osyris, and Thesium* in South India.
2. *Santalum album*, its geographical distribution and accompanying flora.
3. Historical summary of work on sandal haustoria.
4. The external appearance, form and size of the haustoria.
5. Sandal seedlings and their root development in sand and vegetable mould. The first appearance of the haustoria and their region of activity. Cases of self-attachment.
6. First stages of development: the differentiation of nucleus and cortex.
7. The regions of mother root and haustorium proper. The formation of cortical folds. Root hairs on the haustorium.
8. The structure of haustoria which have not encountered a foreign root.
9. The structure of haustoria meeting soft substances.
10. Additional efforts at penetration. Compound haustoria and the formation of secondary cortical folds.
11. Distant action of the haustorial cells. The region of haustorial activity in the sandal root.
12. The occurrence of secreting glands in haustoria.
13. The first appearance of the gland.
14. The structure of the gland and its cells.
15. Lines of growth in the haustorium. Internal changes and the formation of procambium.
16. The formation of collapsed or separation layers in the cortex.
17. The means adopted to effect an entrance into the root attacked: pressure, and the secretion of ferments.
18. The penetration of the host's bark by the sucker.
19. Cases described of haustoria in the act of entry. The further development of the haustorium outlined.

PRESENT PAPER.

1. Summary of the work in the first paper.
2. The formation of the sucker lobes. Description of a young haustorium just entered.
3. Formation of vascular strands in the young haustorium.
4. Structure of the mature haustorium.
5. Need for sections in various directions, transverse, horizontal, vertical.
6. Description of the diagrams of sections through various planes drawn on plate IV.

THE CORTEX AND NUCLEUS.

7. The outer cortex.
8. Inner cortex and nucleus.

THE VASCULAR SYSTEM.

9. The vascular system in the transitional region and in the interrupted zone.
10. The vascular system in the lower part of the haustorium.
11. Secondary thickening: duramen and discoloration.

THE SUCKER.

12. The sucker and its structure.
13. Structure of the haustorial contact cells and their action on the neighbouring tissues.

CASES OF IRREGULAR PENETRATION.

14. Attacks on the cortical wings of the host.
15. Penetration of the wood.

THE GENERAL ACTIVITY OF THE HAUSTORIUM.

16. Excessive activity.
17. Dead or moribund haustoria.

INTER-RELATIONS OF PARASITE AND HOST.

18. Resources of the haustorium.
19. Resistance by the host in its cortical tissues.
20. Protection by the host of its vascular system against the action of the sucker.

APPENDIX I.—List of Sandal hosts.

APPENDIX II.—Some Typical Plants of the True Sandal Zone in Mysore.

NOTE.

SINCE writing the present paper, one or two facts have come to light which may be mentioned here. My botanical assistant, Mr. C. Tadulingam, who was responsible for the finding of haustoria in *Cansjera Rheedii* in the first instance, was sent on a collecting tour to the Nallamallai hills in the north of this Presidency. He was successful in proving that *Ximenia americana* is parasitic in nature. Its haustoria are distinguished by their enormous size and their great enveloping growth, the host's root being frequently hidden in their embrace. He also observed that *Opilia amentacea*, another of the Olacineæ, is a root-parasite. From a cursory examination of the material collected, it is evident that the haustoria in these two species are built on practically the same lines as that of *Santalum album*. They are both provided with glands similar to those in the sandal. In *Thesium Wightianum* there is also a well-defined gland, but the haustorium, although resembling that of Santalum, is of a much simpler nature. *Osyris arborea* and *Cansjera Rheedii*, other root-parasites, have not been as yet sufficiently studied to prove the presence of the gland, but their haustoria are closely allied to that of the sandal, and it is therefore probable that the gland will be met with on further search. Differing from these six is the haustorium of *Olax scandens*, now undergoing detailed examination. Not only is the gland much more complicated in its structure than that of the rest, but there is no medulla or pith in the axis of the haustorium, there being a single median plate of vessels in place of the two broad bands found elsewhere.

MADRAS,
25th November 1906.

STUDIES IN ROOT-PARASITISM.

By C. A. BARBER, M.A., F.L.S.,

Government Botanist, Madras.

THE HAUSTORIUM OF SANTALUM ALBUM.

2. THE MATURE HAUSTORIUM.

1. In the previous paper on this subject* attention was first drawn to the occurrence of haustoria on the roots of certain *Olacineæ* as well as on those of the *Santalaceæ*. Collections of such haustoria having been made in South India, those of the sandal were chosen for description first, because of the economic importance of that plant. A brief statement was made as to its uses and geographical distribution, and a short summary was given of previous work on the structure of its haustoria. The external appearance, form and size of the organs were considered, as well as their mode of origin on seedling roots. It was pointed out that in these, as well as in haustoria of other plants, self-attachment was not infrequent.

The development of the sandal haustorium was then traced by selected examples, beginning with those simple cases where no foreign root was encountered, and passing on to such haustoria as had succeeded in penetrating foreign roots. The tissues were seen to be divided into those of the mother root and the haustorium proper, and, in the latter, into an axial or nuclear and a peripheral or cortical region. In cases of non-success,

* C. A. Barber, Studies in Root-Parasitism. The Haustorium of Santalum album. 1. Early stages, up to Penetration. Memoirs of the Department of Agriculture in India, Vol. 1, No. 1. This paper will be referred to in future as Part I.

additional efforts at penetration were noted, including the formation of compound haustoria and the development of a ferment-secreting gland. The gland was then described, including its development and mature structure. The lines of growth in developing haustoria were considered and the internal changes which these indicated. The formation of procambium and the differentiation of "separation" or "collapsed layers" was described.

The means adopted by the haustorium to effect an entrance were detailed. Cases were figured where the sucker was in the act of penetrating the bark of the attacked root, and the further development of the haustorium, being outlined, was left to a second paper. The present paper may be regarded as a direct continuation of this study, and the former paper is therefore referred to in the text as Part I.

2. When penetration has been effected, the meristematic tissue of the haustorium becomes restricted to certain definite regions, and the rest rapidly assumes the character of permanent tissue. Cell-formation takes place only at the sides of the nucleus and at the lower end of the sucker.

The sucker is pressed against the xylem of the host's root, the woody cylinder, its cells divide rapidly, and it becomes much thickened. The result of this thickening is that the portions of the host's bark on each side of it are thrust apart and form two wings, while the sucker itself, continuing to grow, forms a mass of meristematic tissue under pressure. This mass grows out as two lobes in contact with the xylem, in that the newly formed tissue seeks the line of least resistance for its expansion, namely, on either side along the cambium.

These facts are clearly shown in the section drawn in Plate I, where a young and active haustorium has pierced a root of *Alangium Lamarckii* and is assuming its mature form.

The haustorium here is comparatively large and is still composed in the main of protoplasmic cells. The cortical folds are well developed and tightly grasp the attacked root for

two-thirds of its diameter, while the sucker has reached the wood and has there divided into a broad two-lobed process. The edges of the lobes are provided with actively secreting cells, which have completely destroyed the cambium for some distance beyond their termination.

The bared woody cylinder is closely invested by absorbent cells along which fluids are doubtless beginning to pass from host to parasite. There is no trace in this section of the former presence of a gland, penetration having been effected without its aid.

The nucleus, *ab*, is very clearly distinguished by the smallness of its cells from the tissues around it. At its sides can be traced the procambial strands with narrow, elongated, turbid cells, while above, a darker band of compressed cells separates it from the somewhat larger cells of the transitional region. The elongation of the cells of the nucleus in its lower sucker end, *b*, is well seen, while the cells at its upper extremity remain small and isodiametrical and are beginning to lose their contents.

The cells of the cortex are gradually becoming permanent tissue, but those within the collapsed layers are very different from those without. These collapsed layers, *cl*, are very distinct and are clearly made up of masses of compressed cells whose walls are still to be distinguished but all of whose contents have already disappeared. They formed well-marked separation layers, and the lines of growth in the cortex, formerly continuous (Part I, Plate V, fig. 22), are completely interrupted by the unequal growth of the tissues on either side of them.

In the outer cortex the curves of growth are comparatively unaltered and indicate the direction in which the cell divisions have taken place, namely, downwards and around the attacked root. The inner cortex has, however, become divided into several well-marked regions, depending on the forward growth of the sucker. The cells in the lower part are not readily distinguishable from those of the nucleus, and form no inconsiderable part of the sucker on either side. They have become much elongated in its downward growth. The rest of the inner cortex

varies in appearance according to its nearness to the wings of the host's bark. The upper part consists of very large starch-filled cells arranged in rows, *e*, while those adjoining the sucker are compressed, distorted or ruptured according to their position, as is shown somewhat clearly in this and the two following figures. Plates I—III.

No vessels have as yet been formed in the sucker, thereby indicating that no rapid passage of fluids is taking place. Vessels usually make their appearance first in the transitional region, their function being presumably to pass nutriment to the developing cells of the sucker. These are well shown in the present section, and it is easy to see that, although their junction has not been cut through, they are continuous with the vascular system of the mother root. The latter is seen entering the haustorium above on one side.

3. The section next figured, of a sandal haustorium fixed on a root of *Sida rhombifolia* (Plate II, fig. 1,) shows a somewhat later stage in the development of vascular tissue.

The axial portion of the haustorium, consisting mainly of the nucleus, is unusually broad, and the haustorium is comparatively young. At the junction of nucleus and cortex on either side a definite strand of vascular elements has been formed, consisting of narrow vessels with scalariform markings. The whole of the procambial layer has not, however, been used up in their formation, and a thin-walled cambium-like layer remains outside each strand of vessels for the further development of the vascular system. In older roots this layer assumes the character of ordinary cambium and a succession of vessels is formed, following one another from the divisions of the same mother cells, being thus arranged in regular radial rows. The strand of vessels on each side divides as it approaches the woody cylinder of the Sida root, the presence of vessels at any place presumably indicating the line along which fluids are more rapidly passing.

The sucker is two-lobed, and the lobes are passing along the cambial line. The edge of each lobe consists of cells rich in

protoplasm, which are seen to separate and spread out in a fan-like manner. Around the ends of these cells and between them when they are separated, a clear yellow mucilaginous mass is to be noted.

In the axis of the nucleus the cells in contact with the woody cylinder show by their arrangement that a gland was formerly present in the haustorium, *gl.* All traces of secretion have long since disappeared and the lining cells are pressed together by the swelling of the joining tissues, completely closing the lumen of the gland.

The nucleus is, as is usual in this stage of the haustorial development, clearly marked off above from the transitional region, and the cells in its upper part are small and uniform parenchyma.

The cells of the inner cortex are, as in the previous section (Plate I), readily divisible into different regions. Those in the upper part are large and filled with contents, but the lines of growth marked in the earlier stages are less readily detected. The tissue as a whole is becoming distorted and irregular and has the appearance of dying cells. The cells in the lower part of the inner cortex, namely, those on either side of the wings of the host's bark, are chiefly interesting from the clear manner in which they have recorded the directions in which the growth of the sucker has taken place. From the angle formed by the edge of the sucker lobe in the root attacked, right round to the lower end of the collapsed layer, the inner cortical cells in contact with the wings of the bark are arranged in compressed tangential lines, and present an epitome of the pressures exerted by the wings as they have been forced apart, and the tearing action of the elongating sucker upon the tissues around it.

The tissues of the outer cortex are fast losing their contents. Large vacuoles are present and their protoplasmic (?) contents are irregularly bundled along the walls. The cells are evidently moribund. The cells of the transitional region are less altered, especially in the neighbourhood of the vascular strands, but,

even here, they have ceased to divide and have as a whole become permanent.

A glance at the section in its upper part will at once show that the haustorium has not been cut in the middle line throughout. The vessels and cambium-like layers of the sucker are continuous upwards into the transitional region, but soon pass out of the section. It may be noted that the cells of this transitional region within and without the vascular loop are very similar to those of the cortical tissues, calling to mind the earlier stage, when the nucleus first appeared as a distinct area in the surrounding ground tissue. This will account for the sharp line of demarcation between the cells of the nucleus and those on both sides and above (compare Part I, Plate II, figs. 10 and 11, with Plate II).

4. By our consideration of the successive stages in the development of the sandal haustorium in the preceding paragraphs, the way has been opened for the intelligent study of the mature organ. The main objects of the parasitic attack have been specified, namely, firstly, the rupture and penetration of the host's root as far as the wood, and secondly, the formation of a channel of communication between that wood and the vessels of the sandal root. A mature haustorium cut across is shown in Plate III, where both these objects have been fully attained. The root attacked is one of the orange, *Citrus Aurantium.*

Penetration has been successful along the cambial line. The lobes of the sucker are well developed, and the wings of the host's bark have been thrust back by the increase of the sucker in thickness, so as to gape widely. The vascular system is fully formed and the line of transport is clearly defined, but, with the exception of the tissues adjoining the vascular strands, most of the cells of the haustorium are moribund or dead. Activity is now confined entirely to the absorptive region of the sucker and the united vascular systems. The clasping folds, moreover, are much crumpled on their outer margins ; their ends have ceased to grow, and

their gripping action has been transferred to the sucker lobes within. The folds have thus assumed the purely protective function of a layer of bark.

With this change in function of the outer cortex, the axis of the nucleus has become a sort of pith or medulla, the cells being dead and emptied of all contents. A distinct cambium passes direct from the sucker to the mother root, and outside this the living cells of the inner cortex and transitional region form a protective sheath. The rest of the cortex both within and without the collapsed layers is empty, crushed and dead. The haustorium, as a whole, has thus assumed the character of a transmitting organ, with zones of tissue similar to those met with in ordinary roots.

5. But, in order to understand the structure of the mature haustorium of the sandal, it will be necessary to study sections cut in other directions than those thus far figured. As has been already intimated, the form of these organs is that of a flattened cone, the diameter parallel to the length of the attacked root being considerably longer than that across its thickness. This bilateral form of the haustorium is accompanied by profound differences in structure along the two directions. That such differences must exist becomes at once evident when we consider the nature of the root attacked. The "lobes of the sucker" thus far described are in fact cross sections of two curved lamellæ which, like two hands, separate the bark from the wood on the two sides and lie in the cambial plane. The haustorium must therefore be studied by sections cut in three planes at right angles to one another before we can arrive at any knowledge of its complete structure.

It has been found somewhat difficult to find suitable terms in which to express these three directions, for we have to consider two entirely different organs, the haustorium and the root attacked. If we consider the haustorium alone, it is possible to cut it across at different levels between the mother root and the sucker. All such sections would be called transverse. But sections cut longitudinally might be along the longer or shorter axis,

and these will differ greatly in their appearance. All sections thus far considered have been longitudinal along the shorter axis of the haustorium.

If, on the other hand, we consider the root attacked, a radial organ, we have no such difficulty, the sections being transverse, radial or longitudinal, and tangential. But this is not altogether satisfactory, and I propose to speak of the *whole complex of root and haustorium as it lies in the ground.* We have then transverse, horizontal and vertical sections as follows:—

The *transverse* section is that cutting the root attacked across while the haustorium is cut longitudinally along its shorter diameter.

The *vertical* section will cut through both root attacked and haustorium longitudinally, the latter along or parallel to its longer diameter.

The *horizontal* section will cut the root longitudinally or tangentially and the haustorium transversely.

The first of these sections, thus far alone considered, is by far the most instructive because, on account of the bilateral character of the haustorium and the radial character of the root, it will include all the tissues met with in the two organs. It will now be necessary to consider briefly the arrangement of the tissues in these three directions, the transverse, the vertical, and the horizontal.

6. Such a consideration will be helped by an examination of the figures collected on Plate IV. Although somewhat diagrammatic, each of these drawings is based upon an actual section. The haustorium is first represented as in a model halved across its shorter diameter, and it will be seen that the stage selected is one similar to that shown in the last plate, a mature haustorium which has successfully penetrated along the cambial line. The remaining diagrams on the plate, excepting No. 5, may be regarded as taken out of this same haustorium, although, as indicated above, they represent the study of a great number of different cases.

Transverse Sections, Nos. 2-4.—For all the tissues of host and haustorium to be met with, the section must be transverse, and, for the connection with the mother root to be introduced, the median section should be aimed at, although even then it is not easy to hit the exact line. The connection of vessels of haustorium and mother root is indicated in diagram No. 2, and, as this section shows more of the tissues than any other, the lettering in it is followed throughout, *m*, mother root, *tr*, transitional region, *cl*, collapsed layers, here four in number, two cortical, one at the upper boundary of the nucleus and one axial down its middle, *n*, nucleus, *v*, vessels, *ic*, inner cortex, *cf*, cortical or clasping folds, *sl*, sucker lobes, *w*, wood and *b*, bark of the root attacked.

As the transverse sections recede from the median line, certain changes are to be noted. The instrusion is deep for a considerable distance, the sucker being thickest in the middle section and gradually thinner as each side is approached, with the result that the wings of the host's bark are less widely separated (compare Nos. 2, 3, 4). The differences in the upper part of the haustorium are much more pronounced, for, as will be seen from No. 1, the point of attachment of the mother root is comparatively slender, and the haustorium quickly slopes away. In No. 3 a section is shown half way between the median line and the end of the haustorium. All trace of the mother root and the transitional region have disappeared and the collapsed layers on the two sides are united into an arch right round the top of the vascular system. The upper bundles are cut across as they pass tangentially towards the median line. No. 4, lastly, represents a section cut across one end of the haustorium, whose position is indicated by this numeral in diagrams 1 and 11.

Horizontal Sections, Nos. 5-10.—A figure has here been inserted which does not belong to this series, namely No. 5. It is from a section through a young haustorium not yet penetrated but furnished with a gland, such a stage in fact as is shown in Part 1, Plate V, fig. 22. The gland is seen as an elongated slit in the long axis of the haustorium, and, according to the level at which the section is taken, this split is widely gaping and filled

with mucilaginous rods or tightly closed, in both cases being lined by a well-marked epithelium. The region here figured is that of the "duct."

Reverting to the haustorium now under consideration, a study of diagram No. 2 will at once show that horizontal sections will vary much at the different levels. A number of parallel lines have been drawn through this diagram to show the planes along which the sections shown in diagrams 6—10 have been taken. The lettering is the same in these as in the transverse section mentioned.

The changes which take place in the arrangements of the tissues may be summarized as follows. The mother root may enter at any point at or near the apex of the haustorium. It consists of a central vascular strand with a "bark" which we need not here consider. The vessels, on entering the transitional region, immediately spread out to form a circle, at the same time becoming divided into definite bundles separated by tissues comparable with primary medullary rays. This is shown in Nos. 6 and 7. In structure the transitional region, as shown in No. 7, presents the appearance of a young dicotyledon stem. Passing downwards, the ring of bundles soon spreads out and fuses, becomes flattened into two bands which part at their ends, and the structure shown in No. 8 is reached. It will be seen that, with these changes in the transitional region, the number of vessels has greatly increased. This increase stands in close relation with the enlargement and alteration in the form of the haustorium, whose section becomes more and more oval. The great widening of the vascular loop shown in diagram No. 2 in the transitional region is probably caused by the necessity for accommodating the increasing number of vessels as yet arranged in a circle. The narrowing of the loop below in transverse section being accompanied by the elongation of the whole figure and the rearrangement of the vessels into two parallel plates. Hence the hour-glass shape of the vascular loop in all haustoria of this type.

In No. 8, this rearrangement has been completed. The collapsed layer down the axis of the moribund tissues of the nucleus

is seen, the two vascular plates with radially arranged elements are readily distinguishable, on one side the upper end of the host's bark, *b*, appears, while the two collapsed layers surround the whole, separating the inner from the outer cortex.

The sucker plunges down into the host's tissues, throwing the wings of bark widely apart. In diagram No. 9, these wings are cut across at their base, *bb*, each being clothed on its outer surface by the ends of the clasping folds, *cf*. The sucker has broadened out in the middle and the bands of vessels have broken up into isolated strands, one median and two lateral, in somewhat the manner shown in No. 2. The collapsed layers are seen on the inner sides of the cortical folds. Diagram No. 10, lastly, shows a section through the wood of the host beyond the end of the sucker in the median line. The two sucker lobes, *sl*, are still seen at the sides, working along the cambium which they have destroyed, and the ends of the cortical folds, each with its collapsed layer, are seen symmetrically disposed outside.

These figures have been considered sufficient to indicate the arrangement of the tissues of the haustorium from the mother root to the woody cylinder of the host. There are many stages in between, and some of them very puzzling ones, for it is rare, in horizontal sections, to obtain symmetrical results, a fact indicating once more the plasticity of the whole organ and its readiness to take advantage of any unevenness in the host's tissues and to pass along the line of least resistance in its penetrating course.

Vertical Section, No. 11.—A study of diagram No. 2 will show that an accurately median section through both haustorium and root attacked would show few vessels, and, in fact, would pass through the dead and torn cells of the collapsed layer down the axis of the nucleus. A comparatively thick section has accordingly been selected which passes through the mother root and down the edge of one of the two great vascular lamellæ of the nuclear region. The figure speaks for itself. The collapsed layer at the top of the nucleus is very clearly seen, but the cells of the nucleus, no longer living, and very transparent, are repre-

sented by a clear space. Below this upper part of the nucleus the vessels come into view and pass right down till they meet the woody cylinder of the host. Note especially the way in which the ends of the sucker, where its two lobes unite on either side, project much as they do in the transverse section under the edges of the host's bark, while the clasping folds similarly extend beyond the split which the sucker has made. A reference to diagrams Nos. 1 and 4 will assist in explaining the structure of the haustorium viewed from this point.

We shall now proceed to the study of the structure and further development of the various parts of the haustorium. The cortex and nucleus show certain points of interest and are by no means uniformly developed. These will be briefly dealt with first, after which the vascular system and sucker, the most important parts of the mature haustorium, will receive a special and more detailed examination.

The Cortex and Nucleus.

7. The cortical folds, formed as we have seen principally from the outer cortex, are developed early in the life of the haustorium, probably as soon as a foreign body is encountered (Part I, para. 7). The chief function of these folds appears to be to seize the root attacked and to prevent its being shifted before penetration has been effected. That there is some danger of this occurring may be at once seen from a study of Figs. 7 & 8 on Plate I of Part I, where the root of the sandal and Osyris has gone on growing in length after attachment has taken place. And a little thought will show that with young roots growing in various directions such shifting of position must frequently occur unless forcibly prevented.

The firm attachment of the cortical folds serves another purpose however. The tissues of the outer cortex, ceasing at an early stage to grow and becoming permanent, limit the space in which the swelling of the growing nucleus can take place. One result of this is, as we have seen, the formation of the collapsed

layers, but another is that the downward pressure exerted by the nuclear tissues enables the sucker to throw itself forcibly into any crack or rupture of the host's bark (*cf.* Part I, Paras. 18 & 19).

In transverse sections the growing edges of the cortical folds assume the appearance of ordinary vegetative growing points (Part I, Plate V, Fig. 22), the cells being full of protoplasm and remaining meristematic long after the rest of the cortex has lost its plasticity. There is a frequent tendency in the cells of the part adpressed to the bark to grow out as papillæ, a character assumed by all the external tissues of the young haustorium (*cf.* Part I, Para. 9, and Plate III, Fig. 15). The cells of the growing edges of the cortical folds do not appear as a rule to be actively secreting, but occasionally the formation of masses of yellow secretion altogether similar to that produced at the edges of the sucker lobes seems to indicate that this part also sometimes has the power of secretion and absorption.

Although the presence of this secretion is uncommon, the edges appear to be very closely adherent to the bark. This is seen not only in the actual contact and the close fitting of the folds into all the unevennesses of the surface, but in the pieces of bark torn off, when the cortical folds no longer remain in contact with the root (Part I, Plate IV, Fig. 18). In many cases also the edges of the folds show a very definite *burrowing* action into the outer layers of the bark. In some cases, indeed, where the host's bark consists of thick masses of soft cork, the edges of the folds are seen to push their way between these layers (Plate V, Fig. 3). From all this, we judge that there is considerable force exerted by the clasping folds upon the root attacked, and this is well illustrated by the occasional distortion of young roots (Part I, Plate V, Fig. 22).

In an interesting section through the root of *Ficus mysorensis* the cortical folds are seen to be lifting back masses of bark from the middle line and thus exposing the tissues to the action of the gland and its secretion. While this action has not been observed in other cases, there is no doubt as to the occasional

shearing action of the inner sides of the folds. This is admirably shown in the figure, where a piece of bark of *Albizzia amara* is rolled back like a carpet, owing presumably to the growth of one of the folds subsequent to its attachment to the bark layers (Plate V, Figs. 2 & 2^1 *bk*).

The outer surface of the cortical folds is frequently seen to be thrown into a number of ridges as if this part of the haustorium continued to grow in length after the rest had ceased. It might be suggested that this appearance was due to the shrinking of the central core of the fold in the region of the collapsed layers after the outer portions had assumed their permanent form. But neither of these explanations is satisfactory. In the first place, it has been shown that the outer parts of the outer cortex are the first to take on permanent characters and, in the second, there is nothing to warrant the suggestion of the shrinking of the collapsed layers, since this would of course throw the inner surface into folds as well and cause alterations in the internal tissues which do not exist. It seems on the whole most probable that the formation of corrugations in the outer surface of the haustorium is due to the natural collapse of the cortical tissues, just as creases are formed in a burst bladder, and this suggestion is supported by the appearance of irregular minor collapsed layers outside the main pair in the cortex of the haustorium as well as in the ordinary sandal root.

The cells of the outer cortex as a whole rapidly become permanent, the growing edge alone retaining its power of cell divisions for some time longer. It sometimes happens, however, that the cells within the collapsed layers in contact with the wings of the host's bark retain their vitality for some time. When this occurs, secretion and even penetration may take place anew, but the cells of this part usually early assume the appearance of a defunct palisade parenchyma (Plate II). More remarkable is the occurrence outside the collapsed layers and away from all tissues of the host of what appears to be a well-defined secondary tissue. It appears to be of special occurrence in one or two species of plants and has been observed in some half dozen in all. *Pithecolobium dulce* and

P. Saman show this tissue persistently. It is probably a portion of the outer cortex which remains meristematic after the layers outside it have become permanent and thus retains the early radial arrangement of its cells (Plate V, Fig. 1, and Plate IX, *me*). It was found in six roots of the former species, and a similar meristem has been noted in (garden) *Panax*, *Tecoma Stans* and *Pupalia atropurpurea*.

The colour of the sandal haustoria, when dug up, is uually creamy or light brown, but in some of the older ones this gives place to a rich red brown similar to that of older sandal roots. This is, as might be expected, due to the formation of cork. Cork is by no means usual in sandal haustoria, and in fact the normal haustorium may be described as devoid of it altogether. It is found in a few cases as a layer of brick-shaped cells under the epidermis (Plate V, Fig. 1, *ck*) but more usually as a brilliant red-brown border the elements of which are difficult to separate. With a little perseverance, fortunate places may be found where its true nature can be made out. It is probable, therefore, that the cork-formation early ceases and, as in the collapsed layers, the individual cells are crushed into a non-recognizable refractive mass (Plate VII, *ck*.). An unusual case is shown on Plate VII, Fig. 1, where, in a horizontal section through a haustorium on *Clausena indica*, there is a very great development of cork (*ck*) deep in the tissues of the cortex.

The corky covering of the haustorium usually ceases at the end of the cortical fold, but this is not always so. In a few cases the cork has been noted along the inner side of the fold to the end of the wing of the host's bark (Plate XII, Fig. 1, and Plate V, Fig. 1). Lastly, in one case (*Blepharis boerhaaviæfolia*) the cork was seen to pass right inside the wings and actually to extend to the woody cylinder of the host, the whole of the haustorium being, so to speak, hermetically sealed except at the point of entrance of the sucker.

The last-named exceptional case reminds of what takes place in *Buckleya quadriala*. Here cork is normal and is formed right round the unpenetrated parts of the haustorium. But it does not cease there. In old cases where secondary thickening has

taken place, successive layers of cork are formed cutting off the previous ones and other parts of the outer cortex until the whole of the cortical folds have been thrown off. The old haustorium of *Buckleya* is described as devoid of cortical folds.* This is never the case in the sandal, the folds remaining permanently attached to the host's bark.

8. The inner cortex and the nucleus, forming together the axis of the haustorium, are less interesting, as such, in the mature organ. In fact, a new sub-division of the tissues will be convenient. The lower portion of the axis, consisting chiefly of nucleus but also of inner cortex, has become the sucker, and this deserves special attention. In the upper part including the transitional region, which has not penetrated the host's root, all tissues rapidly become permanent and the interest centres in the vascular system.

Reserving then the sucker and vascular system for separate examination, we may briefly consider the fate of the remaining parts. The arrangement of the various collapsed layers and the lacunar tissue is perhaps the most striking feature at this stage of development. The nucleus has, as we have seen, a transverse band of crushed cells across its upper end and, in older haustoria, a layer of collapsed cells appears down the median line (Plate IV, diagram 2), but these are of less interest than the system of collapsed or separation layers in the cortex.

Ignoring the outer, irregular ones referred to in the last paragraph, there are a pair of *collapsed layers* which are a constant feature in all haustoria of this type. These form true separation layers dividing the inner from the outer cortex. They are terminated upwards in median sections at a point opposite to the increase in diameter of the vascular loop (Plates I, II, III, and Plate IV, diagram 2). This is to be noted, for it constitutes one of the differences between this haustorium and that of

* S. Kusano, Studies on the Parasitism of *Buckleya Quadriala*, B. et H., a Santalaceous Parasite, and on the Structure of its Haustorium, Journal of the College of Science, Imperial University, Tokyo, Japan. Vol. XVII, Article 10.

Olax. The downward ending of the collapsed layers is at a point on the inner side of each cortical fold just short of its edge. Opposite the middle of each collapsed layer, on its inner side, a well-marked lacunar tissue is formed at an early stage of haustorial development (Plates II and III). Later, on either side of this lacunar tissue, the cells become crushed and form strands, at first irregular, but afterwards simulating true collapsed layers. The whole of this part of the inner cortex ultimately becomes a collapsed layer projecting inwards and downwards from each primary one (Plate IX and Plate XIII, Figs. 1 and 2). The downward extension is carried comparatively close to the inner side of the wing of the host's bark. As is usual with separation layers, the tissues on the two sides of these downward prolongations are different in form and history, the cells next to the host's tissue, at first absorptive, becoming empty and moribund, while those on the other side form the outer part of the active tissues of the sucker. It is noteworthy that wherever the host's tissues are approached by those of the haustorium, whether as islands (Plate XI, Fig. 2) or otherwise, sooner or later the haustorial cells in contact with the host are separated from their neighbours by a collapsed layer.

When a compound haustorium is formed, there are a pair of collapsed layers in each cortical fold (Part I, Plate III, Fig. 15, and Plate IV, Fig. 18). The upper parts of the cortex in such haustoria, even when they are comparatively imperfectly developed, are no longer active, being superseded by the secondary folds. The tissues in the upper part have become permanent and, in fact, have developed the inward projecting secondary collapsed layers just described. It is interesting to note that these layers are ultimately continued downwards into the new cortical folds, and there form the pair of collapsed layers proper to them (Plate XIII, Fig. 1).

It is easy to see that a careful study of these collapsed layers will throw much light on the series of changes in growth and pressure in the haustorial tissues. But this study is not justified here, and it must suffice to refer the reader to the various figures

indicating the general position of these layers in the older haustorium.

The arrangements here described are those seen in median sections through the length of the haustorial axis. A section slightly on one side shows the united collapsed layers passing right round the vascular loop as a sort of sheath (Plate IV, diagram 3, and Plate XVI, Fig. 1). Further from the middle, the collapsed layers disappear altogether (Plate IV, diagram 4). And a careful study of the different diagrams of transverse, horizontal and vertical sections contained in Plate IV will enable us to build up a complete model of the haustorium and the distribution of the collapsed layers.

Vascular System.

9. For the study of the vascular system of the sandal haustorium it will be necessary to secure sections in all the three directions referred to in paragraph 5.

A good general idea of its course may be obtained from a study of the transverse section figured on Plate III of *Citrus Aurantium*, and it will be seen from that figure that there are great changes as we pass from one part to another. An examination of the cross-sections of the vascular strands will have to be made at different levels and a series of horizontal sections will have to be called into requisition. This will be rendered clearer from a study of the diagrams on Plate IV, especially Nos. 2, 6—9, 3 and 11.

Speaking generally, the vascular system may be conveniently divided into three regions. In its upper part it belongs perhaps strictly to the mother root and, as far as the line 7 in diagram 2 of Plate IV, is of little interest. Below this region, however, a series of remarkable changes take place, and, just at the point of change, where the vessels seem to become disorganized or to altogether disappear, a very careful study will be necessary. Proceeding downwards from this point along the wine-glass-shaped course of the vessels, the main mass of the haustorium is reached and the vascular structure is more or less

definite. In the sucker a second disintegration takes place and the vessels become distributed so as to apply themselves to the various woody elements of the host's root.

The direction of transport being from this woody cylinder to the mother root, horizontal sections will cut the various elements across. The true relations of pith, procambium and its outcome cambium and secondary wood, and the cells outside the latter can be best studied in such sections.

Commencing with the transitional region (between the lines 6 and 7 in diagram 2 of Plate IV), the bundles cut across are seen to be arranged much as in the mother root. And it may be noted in passing that there is little difference here between root and stem structure. A series of isolated bundles are seen to surround a central "pith," with xylem elements within and softer, phlöem elements outside, the whole being surrounded and separated from the "cortex" by a more or less distinct "sheath." Such a stage is shown at *a* in Fig. 1 of Plate VI, where a haustorium fixed on *Citrus Aurantium* is cut across in its upper part.

In these bundles there is a clear distinction between the protoxylem, with vessels scattered irregularly and isolated thin-walled parenchyma between, and the more closely arranged secondary wood with rows of vessels and well-marked medullary rays.

Horizontal sections through a haustorium rarely cut that organ accurately across, and most are very oblique. Advantage has been taken of this fact to include in the same figure two different regions of the vascular system. Thus in the section above referred to (Plate VI, Fig. 1) as well as that lower down on the same plate, while one side of the haustorium represents one part of the vascular tract, the other shows a somewhat lower region.

Passing down the transitional region the circle of bundles expands and becomes oval, and both vessels and bundles increase in number. This will be understood from a glance at diagram 2 in Plate IV. But, with this change, another takes place which is more difficult to explain. The vessels become less clearly defined and assume a yellowish colour, at any rate in sections through spirit material. Newly formed and active xylem appears dark in

thickish sections because of the optical properties of the walls of the vessels, but as we proceed down the transitional region, the xylem becomes more hyaline and assumes a yellowish colour. This is well seen in the lower half of the section under examination (*b* in Fig. 1 of Plate VI) where, owing to the spreading out of the vascular loop, the vessels are cut obliquely. It may be noted that the lower part of the figure is also obviously through a lower part of the haustorium because the first indications of the collapsed layer, *cl*, are met with between the vascular circle and the periphery. The change here indicated rapidly becomes intensified until the circle of vessels becomes widely oval, is no longer collected into definite groups of vessels, but presents a band of tissue with scattered vessels (Plate VI, Fig. 2, *a* a^1). The exact point at which this occurs is traceable in almost all sections through mature haustoria (Plates III and IX, *iz*) as well as in the diagram No. 1 on Plate IV. The bundles, besides becoming thus disintegrated, assume the yellow colour spoken of above. This colour is seen to be due to changes in the character of the vessels. Their walls become swollen and yellow, at the same time becoming more hyaline, while the interior is filled with a yellow gum-like substance. In many places this proceeds so far that the vessels are completely disintegrated (Plate VII, Fig. 1, *b* b^1).

The region at which this remarkable change occurs coincides with the upper limit of the nucleus (Part I, Plate II, Fig. 11) and with the lower extension of the endodermis, where that layer is discernible. For reasons already given, this point has been assumed to be that of the junction of the mother root and the haustorium proper, of, speaking more correctly, the tissues formed from within and without the endodermis of the original sandal root. In transverse sections the vessels appear as if interrupted at this point, as will be readily noticed by a reference to the figures, and it may therefore be conveniently termed the "interrupted zone" of the vascular system.

While the vessels above and below this point are perfectly normal in appearance, dark in thick sections and clear white in thin, this break in the vascular continuity is difficult to

understand. That it is a regular phenomenon is shown from the figures of mature haustoria in the present paper, but it may be observed that it is also met with in the haustoria of some other plants of this type, and, indeed, it is much more clearly shown in *Cansjera Rheedii*, where also the exact limits of the endodermis, so rarely met with in the sandal, are frequently seen.

It is difficult to understand how fluids can pass from host to sandal root through this region, and this, more than anything else, has led to the assumption that the activity of the haustoria is of comparatively short duration in *Santalum album*, contrasting remarkably with the long-lived organs described by Kusano in *Buckleya Quadriala*. In that plant a similar interruption appears to take place although no mention is made of disintegration of the vessels, but the haustorium continues to grow for years after attachment has been made, keeping pace in its secondary thickening with that of its host. It must, however, be confessed that the true significance of these phenomena has not been fully grasped, and that they present the chief difficulty thus far met with in the study of these complicated organs. It would seem unlikely, on the face of it, that as soon as the haustorium has attained its full form, the passage of fluids should thus be cut off, and in many haustoria the sucker lobes are still to all appearance in full activity and even expanding along the cambial line when the interrupted zone is well marked. It may possibly be that the active cells of the sucker go on growing, and secondary thickening proceeds after all connection with the mother root has ceased, the tissues being fed by the natural products of the absorptive activity of the surface cells of the sucker.

10. The interrupted zone occurs at a place slightly above the widest expansion of the hour-glass-shaped vascular loop. Immediately below it the vessels become rearranged in the reverse manner to that described above. The scattered, decayed vessels are seen to branch freely and give rise to a mass of vessels, at first obliquely cut in horizontal sections, which assume the form of two broad bands of vascular tissue. This is shown in

the Figure 1 on Plate VII of a haustorium fixed on *Clausena indica*. The upper part of the section, at *a*, shows masses of vessels faint in outline and filled with yellow gum, while the lower part, with its strongly marked collapsed layer, shows a lower part of the vascular loop and the formation of a broad band of vessels with well-marked cambium on the outside. On the left hand side of the figure, owing to a fortunate obliqueness of the section, the passage from the tissues of one side to those on the other is clearly shown, *b* b^1, and the change from the yellow, disintegrated vessels to the normal sharply defined condition. This part of the section is more carefully drawn in enlarged Figures *b* and b^1.

The second section on this plate, also of a sandal haustorium fixed on *Clausena indica*, shows yet a further change, in that the narrowing of the vascular loop is indicated. The lower half in this figure (which only represents the part between the two collapsed layers, *cl*) shows a stage somewhat similar to the lower one of the previous figure. Here the vessels are seen to be arranged in a lattice-like manner penetrated by wide masses of parenchyma (Fig. 2, *a*) and their lying longitudinally in the section is explained by a reference to diagram 2 of Plate IV where it is seen that the vascular loop is rapidly narrowing and the vessels are approaching the median line. On the left of this figure the vessels are irregularly cut in various directions, but pass gradually round to the true axial region which is clearly seen on the right half of the upper part of the section, *n*.

We have now passed through the most difficult part of the vascular region, and it may be well to recapitulate. The vessels in the transitional region are arranged in bundles much as in the mother root, in a circle with the elements arranged as in dicotyledon stems. The circle expands downwards and at the same time the vessels increase in number and are no longer arranged in well-defined bundles. After reaching a point where the vessels are all scattered, disintegrated and filled with gum, the interrupted zone, they reunite lower down to a considerably larger vascular complex arranged in two broad bands. The loop now attains its broadest dimension and then rapidly narrows, the vessels being arranged in a

sort of lattice-work and the interstices being filled with parenchyma. Lastly, the vessels close in and form two definite bands, one on each side of the middle line, as shown in diagram 8 on Plate IV.

Such a stage is shown in the section through the axial region of a haustorium fixed upon a root of *Thespesia populnea* (Plate VIII). The arrangement of the individual elements of vascular tissue is here very similar to that described above for the transitional region (Plate VI, Fig. 1 at *a*) with the exception that the protoxylem of each side forms a united band, and is not separated into distinct bundles by primary medullary rays. The axis of the nucleus forms the pith, in the centre of which is frequently seen a line of collapsed cells, cl^1. Abutting on the pith is an internal layer of meristem, *ic*, not derived from the procambium and not always present. The protoxylem is distinguished as usual by the irregular arrangements of the vessels and the scattered parenchymatous cells between them. The secondary xylem arising from the divisions of the true cambium consists of radial rows of vessels with well-marked medullary rays between, although the present section shows a comparatively young stage with few vessels. The cambium, *oc*, is well defined and consists as usual of thin-walled meristematic cells. It is easy to define the limits of the tissue derived from the divisions of each mother cell both inwards and outwards.

There is no true bast in the sandal haustorium, sieve-tubes not having been found in any of the sections. But not infrequently layers of parenchyma, sometimes filled with starch, are found on the outer edge of the bundles. These are generally cells belonging to the cortex, but, in other cases, they are derived from the cambial mother cells (Plates XII, Fig. 1, XIII, Fig. 2, XIV, Fig. 1, and XV, Fig. 1). What the exact function of these starch cells is has not been determined, but it seems probable that their contents are utilized in the formation of further vessels from the cambium. In any case they form a protective sheath between the cambium cells and the moribund tissues of the cortex outside. The latter protective function is also performed by the inner meristem already stated to be occasionally met with, a mass of

starchy cells being also found here, generally only at the upper end of the axial region where the vascular loop begins to expand (Plate III). These details may be followed with advantage in the figures on Plate VIII, with the proviso that the secondary xylem is as yet small and the distinction between primary and secondary has not yet declared itself very clearly. It is difficult to obtain sections in which all the tissues here described are to be found in one and the same place.

Attention is invited to the section drawn on Plate XV, Figs. 1 and 2, where, the haustorium being moribund (?), all the tissues are shown with very clear cell walls and no contents. Here the relations between the cambium, vessels, medullary rays and cortex are very clearly seen in the transverse section. The cortex passes outwards into a collapsed layer, *ic*, which, however, is not the main one but a piece of compressed tissue leading up to it.

The vascular system in the *sucker* is of comparatively less interest, and the terminations of the elements downwards may be conveniently considered when dealing with that part of the haustorium. Soon after the sucker is entered (meaning by "sucker" that part of the haustorium included between the widely separated wings of the host's bark), the two bands of vessels become less sharply marked out. Isolated strands of xylem become detached from the main mass either on the inner or outer side, and soon the whole system becomes separated into individual vessels or small groups which pass to various parts of the woody cylinder of the host's root (Plate IV, diagrams 2 and 3, and Plates II, III, etc.) where the passage of fluids is presumably most active. Ultimately some such stage as that shown in diagram 9 of Plate IV is reached, where the vessels are no longer arranged in any very definite order. Because of this separation of the vessels from one another they are not well seen in any of the transverse sections on Plates XI—XVI.

11. The life of the cambium in the haustorium is comparatively short in *Santalum album*. The cell layers formed from it outwards are usually few in number and are soon terminated by

the cortical tissues. In some cases, however, a considerable mass of secondary tissue is formed in this region. The cells thus formed are parenchymatous, evenly arranged in rows and filled with starch in actively growing haustoria. In the older, moribund haustoria they are seen to be thin-walled and empty (Plate XV, Figs. 1 and 2). This outer secondary tissue assumes its greatest development when the secondary xylem is also thickest.

The upward and downward range of the cambium is not very easy to follow in the sections examined. It may, however, sometimes be traced into the transitional region and it may even extend down to the end of the sucker. In the latter there is sometimes a great development of parenchyma from the cambium outwards, and the lobes in such cases become thick and turgid (Plate XII, Fig. 1).

Secondary thickening or the formation of secondary xylem is not a very marked character in the sandal haustoria as yet examined. On the other hand, it is, in some cases, long-continued, and in this, as in other respects, it varies with the host, the thickening being more pronounced when the haustorium meets with the roots of certain species of plants. The haustoria examined on roots of *Ruellia prostrata*, *Blepharis boerhaaviaefolia*, *Pupalia atropurpurea* all show signs of great activity in secondary wood formation, usually accompanied, as above noted, by an increase in the tissues in the phlöem direction. It is well, however, to note that the best examples of great secondary thickening, both inside and outside of the cambial layer, were met with in roots collected in Madras city, a region outside the natural limits of the sandal, where the growth is abnormally rapid and where the wood is destitute of the valuable oil of commerce. Perhaps, a further study of sandal trees in Madras might bring to light other examples. The bulk of the haustoria collected for this paper were either from mature trees growing in true sandal tracts or pot-plants raised in Madras. An example on *Pithecolobium dulce*, obtained from a well-grown tree in Madras, is quite unique in the amount of secondary wood developed (Plate IX).

We have already noted on several occasions that the growth of the haustorium varies a good deal according to the species of plant to which it is attached. This is nowhere better seen than in species of *Pithecolobium*. In the case figured on Plate V (collected in a true sandal tract) there is a well-marked and unusual formation of cork, *ck*. There is also a very distinct mass of meristematic tissue on the outside of the collapsed layers in the cortex, *me*. An examination of the present section, Plate IX (collected from a mature specimen in Madras) shows the same character. Lastly, there is in both a great development of tissue both outside and inside of the cambium. It would seem from these observations that *Pithecolobium dulce* has this influence on the haustoria attached to its roots that it encourages meristematic growth in all the tissues. And that *Pithecolobium Saman* behaves in a similar manner has already been noted.

Another point to be remarked in the figure is the clear manner in which the wood of the host is altered opposite to the area of contact with the haustorium. A comparison is invited with the case figured on Plate XIV, Fig. 2, where the scar left by an old dead haustorium on the same plant is shown.

In cases where much secondary thickening occurs there is a distinct sign of the formation of a duramen. The inner layers of the secondary xylem, to wit, become brown, and, upon examination, it is seen that this is due to the browning or yellowing of their walls and the appearance of gum in their cavities exactly as in the interrupted layer already described. This formation of duramen is very clearly seen in the section through the root of *Cassia auriculata* figured on Plate XV. The protoxylem does not appear to share in this change. It is separable as a whitish layer of vessels irregularly arranged. Outside the protoxylem the inner secondary vessels are coloured yellow and their cavities are full of globules of a gum-like substance. Further outside again the younger vessels are clear and white, resembling in this respect the alburnum of an ordinary root. These appearances are of special interest when we consider the course of events in *Buckleya Quadriala*. Here, according to Kusano, secondary

thickening takes place for a series of years with the formation of a well-marked duramen, the latter keeping pace in its development with the similar tissue in the aging root to which the haustorium has attached itself. As has been frequently insisted on, the long-continued activity thus indicated does not occur in the sandal haustoria, and it would be interesting to study the roots of *Buckleya* again in the light of the facts brought to light in the present paper. There appears to be a well-marked interrupted zone in *Buckleya*,—are the vessels at this point disorganized as in sandal ?

But, besides the discoloration of the older parts of the secondary xylem, in the search through numerous slides for indications of a duramen, certain cases were encountered in which the protoplasmic elements were seen to be discoloured. The cambium in particular assumed a brownish tinge, while the absorptive and glandular tissues in contact with the woody cylinder were not infrequently dark in colour also. Thus in all sections through haustoria fixed on *Capparis zeylanica* the cambium was light-brown right up to the interrupted zone. It also occurred in *Diospyros montana* and *Cassia auriculata*. There seems to be but one explanation of this phenomenon. The cells of the tissues most actively living have absorbed colouring matter with the fluids taken up from the host. What the effect of this colouring matter is upon the living elements has not been determined. It is probably a purely osmotic phenomenon, but it may also possibly be one of the numerous efforts to be detailed below of getting rid of the intrusive tissue of the parasite by poisoning.

The Sucker.

12. It remains now to deal with the sucker, in some ways the most important part of the haustorium. A full study of this organ, its mode of attacking the foreign root, the double function of secretion and absorption, the effect of its attack upon the host's tissues and their various modes of self-protection or even active resistance cannot be fully described here. We can merely record

the main facts concerning the character and development of the sucker.

As we have already seen in Part I, paragraph 17, the sucker is that part of the growing end of the haustorium which is thrust between the flaps of bark of the host's root when entrance is effected. It consists mainly of nuclear tissue, although a portion of the inner cortex is carried along with it on each side. At first narrow and tongue-like, it rapidly expands, fresh material being hurried down from the rest of the haustorium. Arrived at the woody cylinder, and barred in its further progress by the denseness of that part of the host's root, and continuing to grow and expand, it forces its way along the line of least resistance and passes in two broad lobes along the cambial plane on either side. The wings of the host's bark are thus forced widely apart until they assume a more or less vertical position. This growth of the sucker may be followed by referring to Plates VI—VII of Part I and Plates I to III in the present paper. When the stage on Plate III is reached, protoplasmic activity is concentrated at the lower end of the sucker (as well as along the cambium). This arrangement of the living cells is easy to understand when we remember that, as already pointed out, wherever haustorial tissues come into contact with a foreign body there is an accumulation of plastic material at that point. The region of greatest activity in the sucker is where its cells touch those of the host, and the tissues in its upper and central part quickly assume the permanent character of the nuclear cells above.

The vascular elements, upon entering the sucker, are still disposed in two parallel plates (upper part of diagram 8 in Plate IV). These plates become less regular downwards, break into detached groups or isolated rows of vessels as the tissues of the host's root are approached (Plates II and III), and the ultimate endings become applied to various parts of the woody cylinder. There is little difficulty in tracing the points of origin of vascular elements, as the rows of cells are early provided with reticulated markings on their walls. These, as would be expected, appear at those points where the transport of fluid is greatest, and the

vessels in this lower part of the sucker are accordingly formed at any point, and not along a definite tract as in the region of procambium already described. Wherever absorption is most active, the row of vessels is soon met with. It would naturally be expected that the vessels in the sucker would appear chiefly opposite to the vessels of the woody cylinder of the host, but this is by no means the case. It is not generally possible to trace any close connection between the distribution of the vessels of host and haustorium. The vessels of the sucker are, as a matter of fact, formed opposite to the wood vessels, wood parenchyma, medullary rays or fibres promiscuously.

In one or two cases, however, more or less accurate apposition of vessel to vessel has been noted, and this depends on peculiarities in the structure of the woody cylinder of the species. It has been met with in *Diospyros montana*, *Kigelia pinnata*, *Polyalthia longifolia*, while in *Jatropha gossypifolia*, where the vessels are arranged in radial rows in the transverse section separated by masses of other tissue, the vascular strands of the sucker end up accurately opposite to these. Such cases are rare. An extended study of the whole series of sections examined allows of no forecast as to where the vessels of the sucker will appear in any given case.

Good sections showing the actual point of contact of the vessels of the haustorium and the tissues of the woody cylinder have been obtained in a number of species. There is nothing of importance to remark in these. The vessel of the sucker is terminated at the point of contact by its cell wall in such a manner that the elements of host and haustorium form practically one tissue, although the line of separation is perfectly clear, thanks to the layer of yellowish secretion so often met with (Plate X, Fig. 1). One case of special interest may, however, be noted in passing. In *Gyrocarpus Jacquini*, as in many other species, thyloses are formed in the vessels of the root near the line of contact with the sucker. These thyloses undergo here a remarkable modification when opposed by a vessel of the sucker, in that they become reticulated with markings like those of the

haustorial vessels. It appears from the section as if the ends of the vessels of the parasite actually enter the lumen of the larger vessel of the host. And, in one sense, this may be taken to be really the case. The wood parenchyma surrounding the vessel attacked having been disorganized by the secretion of the sucker cells, the latter are brought into close contact with the pores of the large pitted vessel. Pressure being greater in the sucker cells, thyloses are formed. Later, when the passage of fluids commences, reticulated thickenings are formed upon the walls of the haustorial cells, and these are found both on the parts outside and inside the lumen of the host's vessel. A good illustration of this phenomenon is to be found on Plate V, Fig. 4, *th.*

13. The sucker is in contact with the host on the inner side of the wings and along the exposed surface of the woody cylinder. The cells adjoining the wings of the cortex are at first charged with protoplasmic contents, but their activity is usually short-lived. They then enter upon a resting condition and become separated from the main mass of the sucker tissues by a more or less distinct separation or collapsed layer (Plates I, II, III, XV, etc.). Not infrequently, however, the tissues of the wings show signs of their secretive action, becoming disintegrated in various degrees, but the solvent action of this part of the sucker is far less energetic than of that about to be described.

The cells of the sucker in contact with the woody cylinder, although at first full of protoplasm, undergo a series of changes similar to those at the sides, as age increases. The protoplasm becomes granular, starch grains are formed and increase in number until they nearly fill the cavity of the cells, or the cells become empty and moribund. Presumably the starch-filled cells have ceased from the secretion of the ferment, take no further part of the passage of fluids and have entered upon a resting stage in which they serve as a storehouse for reserve materials. From cases observed, it appears probable that such cells have still the power on occasion to resume activity, to pour out secretion and dissolve the tissues of the host opposed to them. Where the

sucker cells have become empty, it is interesting to note that, long after the rest of the haustorium is decayed and collapsed, forming broken shreds of dead tissue, the cells of the sucker attached to the woody cylinder are clearly distinguishable and persist as a sort of clothing epithelium. From this and other facts of a similar character, it appears possible that the cells of the sucker are capable of being nourished and kept alive by the host's tissues after all living connection with the rest of the haustorium has ceased. And, if this is the case, the fact is explained, why, even after the vascular continuity is broken by the appearance of the interrupted zone, the sucker lobes continue to grow with every appearance of fulfilling their functions towards the parent root.

At an early stage of the attack a clear yellow layer of gummy substance appears to separate the sucker from the host's tissues. The origin of this layer is not in all cases certain. While usually a product of the haustorial cells, it appears probable that in some cases both sucker cells and the host's tissues share in its formation. As has been noted, the sucker, on contact with the woody cylinder, expands and sends a process along the cambial line on each side. The tissues in contact with the woody cylinder may therefore be regarded as in an older stage than those at the end of the sucker, and a study of this latter part proves to be of the greatest interest. The cells at the edge of the lobe become separated from one another and spread out after the manner of root-hairs in a dense mass of yellow substance (Plate X, Figs. 1 and 3). This yellow substance, which is almost always formed in a greater or less degree whenever the haustorial tissue elements encounter a foreign substance, is formed partly from a mucilaginous secretion from the sucker cells and partly from the disorganized walls of the cells concerned. In the gland, as we have seen (Part I, para. 14), the manner in which the secretion is formed is fairly easy to follow. It is much more difficult over the surface of the sucker, but there is some reason to believe that it is intrinsically the same in the two cases. If this is true, then it is also probable that the cells producing the secretion

become disorganized in the process, and that the function of absorption is performed by the cells immediately behind them and which take their place at the surface.

Fig. 2 on Plate X shows the edge of the lobe in a haustorium fixed on a root of *Cordia Myxa*. In it the outer cells have a structure similar to that of the secreting cells of the gland already described (Part I, Plate V, Figs. 25 & 26). Below them the cells are granular and protoplasmic and will presumably take their place, becoming absorbent or not according to the stage reached. The tissues of the host show very clearly the effect of the secretion upon them, their cell walls especially being faint and shadowy. At a later stage the outer cells of the sucker will presumably become absorbent and the cells shown in the next figure, taken from the same section at a short distance from the edge of the lobe, are possibly acting in this manner (Plate X, Fig. 3). A general view of the edge of the lobe and the surrounding tissue is given in Plate X, Fig. 1, which is taken from a section through an attachment on the root of *Casuarina equisetifolia*. At one place, *x*, there appear to be the remains of such a secreting cell as those found in the sections through *Cordia Myxa*.

Such sections as those shown above are, it is true, extremely rare in the series, and the views here expressed as to their general significance are put forward with considerable diffidence. The subject is difficult because of the impossibility of selecting the haustorium to be cut. The work in the ground is, so to speak, comparatively blind, and only by the comparison of a very large number of sections showing suitable stages can any certainty be arrived at.

The effect of the secretions on the host's tissues has been made a matter of careful study, and numerous notes have been accumulated on the subject. It is felt, however, that for the purposes of the present paper a full consideration of these would not be justified. Attention may, however, be drawn to one particularly instructive section where the fact is most clearly shown that the ferment secreted is chiefly concerned with the dissolution of cell walls—is in fact cyto-hydrolytic. No doubt diastatic ferments also exist, but the presence or absence of starch

in the tissues of the host depends on so many other factors that a mere observation of their existence opposite the sucker layers is likely to be misleading rather than otherwise. As a general rule, it may be stated that starch is frequently present in abundance even where the effects of the sucker are most marked.

In the section through a haustorium fixed on a root of *Grewia tiliaefolia* figured on Plate XI, Fig. 2, it is seen that the sucker attacks the inner layers of the wings of the bark as well as the woody cylinder of the host. In the cortex thus attacked there are small, compact strands of sclerotic tissue interposed between the large starch-filled thin-walled parenchyma. Plate II, Fig. 2, shows the junction between the side of the sucker and the cortical wing in another section through the same species. In this section the starch grains are, it is true, ultimately dissolved and, indeed, appear to have been cleared out of certain tracts which have become filled with brown indefinite substance. But the effect upon the walls of the sclerotic cells is much more marked. Bearing further upon the cyto-hydrolytic action of the sucker ferment is the fact that in cases where its action at a distance can be demonstrated, the fibrous strands are much discoloured, while the starch grains in the neighbouring parenchyma are to all appearance quite untouched.*

Cases of Irregular Penetration.

14. The symmetrical penetration of the two lobes of the sucker along the cambial line is usual in attacks upon the roots of dicotyledons. That this would naturally be the case is at once evident when we consider the structure of such roots, a firm, corky bark, a less resistant cortex and a dense woody cylinder. But where this arrangement of tissues does not hold, there are irregularities in the mode of penetration. We have seen that

* Peirce has noted that in *Cuscuta americana* the secretion dissolves the cell wall first and then the contents more slowly. In an attack of *Cuscuta glomerata* on a balsam leaf the cell walls were perforated quickly, but the contents were slowly dissolved, the starch grains first and then the protoplasm. G. J. Peirce, On the Structure of some Phanerogamic Parasites. Annals of Botany, Vol. VII, 1894, pp. 291-327.

where the outer layers are capable of great resistance, the haustorium is, on its side, capable of making a series of efforts at producing a rupture, with the result that compound haustoria are formed. And, with variations in resistant power of the host's inner tissues, the haustorium sucker shows the same plasticity in its development. This is seen in differences in the form of penetration and the character of the penetrating processes.

It not infrequently happens in the roots of tropical plants that the cortex is provided with a series of concentric bands of sclerotic tissue. These offer considerable resistance to the penetrating lobes of the sucker (Part I, Plate IV, Fig. 18). It is not uncommon in cases of this kind for the lobes, following the line of least resistance, to be diverted from their course and to wander tangentially through the cortex. We have seen (Part I, para. 18) that in the various species of *Zizyphus* the sucker is frequently unable to overcome these obstructions, and, after penetrating for a certain distance in an irregular manner, the haustorium has become moribund before reaching the cambium at all. An interesting example illustrating this irregularity in penetration is figured, where, in an attack on a root of *Pterolobium indicum*, one of the sucker lobes is wandering hopelessly between the sclerotic bands of the cortex, while the other has successfully reached the cambial tissues of the host (Plate XI, Fig. 1).

The reason for the one-sided entry in this case is evident in that the lobe has failed in taking the right line. In other cases it is not so easy to state the reason for only one lobe developing, but such cases are comparatively rare in dicotyledons, although occasionally met with.

Attacks by the sucker on the cortex as a nutritive tissue are not common. The usual course is for the haustorium to pierce this tissue as rapidly as possible, and the two wings are thrown back on either side and left gradually to wither away. But cases have been met with where the wings are first thrown back and then forcibly attacked by the secreting tissues of the sucker at the point of contact. If the origin of these tissues is considered

for a moment, this will not appear very strange. Before entry all the parts of the haustorium in contact with the host have the power of secreting ferments (Part I, para. 8), but such powers are usually restricted to the lobes of the sucker once penetration has been effected. In the cases now referred to, the cells in contact with the wings of bark have retained their power for a longer period and, presumably incited by the presence of food material in the bark, have commenced a penetration on their own account. As is so frequent with sandal haustoria, these attacks are much commoner in the roots of certain genera, showing afresh the important influence exerted by the host on the development of the parasite.

Attacks on the outsides of the wings are comparatively rare, the cells of the enveloping cortex of the haustorium quickly losing their vitality. Such have, however, been observed in *Cassia auriculata* where the haustorium appears to attack all parts indiscriminately. The roots of *Grewias* of different species not infrequently show attacks on the wings of bark, these being penetrated by absorbent tissue both at their ends and from the inside (Plate XI, Fig. 2). This phenomenon has also been observed in *Casuarina equisetifolia*, *Guazuma tomentosa*, *Jatropha gossypifolia*, *Melia Azidarachta*, *Parkia biglandulosa*, *Polyalthia longifolia*, *Premna tomentosa*, *Pterolobium indicum*, *Zizyphus Oenoplia*, etc. The roots of *Diospyros montana*, on the other hand, show a well-marked effort of the sucker lobes to cut off the wings of bark at their base (Plate XII, Fig. 1), the activity of the secreting cells being rendered at once evident by the black colour of the cells attacked. This has also been observed in *Capparis zeylanica* and *Ficus religiosa*, while in *Polyalthia longifolia* the wings of bark have been entirely separated by lateral protrusions of the sucker lobes across their bases.

15. The woody cylinder of the roots of dicotyledons is usually composed of vessels closely bound together by smaller thick-walled cells. The wide vessels are so closely invested by bands of small-celled tissue that the cylinder as a whole is

the densest part of the root. This fact, combined with the arrangement of the cambial layers, makes it unusual for the woody cylinder itself to be penetrated.*

But there are not a few roots where the tissues are loose and spongy in the central cylinder. Such are the roots of many climbers and of such plants as *Ficus*, *Opuntia*, *Jatropha* and *Panax*. In these cases the sucker does not confine itself to the cambial line, but passes directly into the wood. Two typical cases are figured showing this action of the haustorium. In *Ficus mysorensis* (Plate XII, Fig. 2) the woody cylinder is irregularly fractured, while in the *Opuntia Dillenii* (Plate XIII, Fig. 1) the wide medullary rays furnish the path along which the sucker has penetrated.

In roots which are still young and when the tissues are not hardened, and in the roots of a more succulent nature all through, the haustorium behaves as it does when it meets with homogeneous soft tissue. We have seen that, in the tubercles of leguminous plants and in a curious attack upon the chrysalis of a small Lepidopteron (Part I, para. 9, and Figs. 15—17, Plate III) the haustorium, meeting with no resistance in any direction, has grown out into a hemispherical mass of parenchyma which tissue has the power of secretion and subsequent absorption. Where roots attacked are of a uniformly soft nature, the sucker assumes a broad form and bores its way into the tissues flattening them out before it in its progress. A good example of this is seen in the figure of a haustorium attacking the root of *Jatropha gossypifolia* (Plate XIII, Fig. 2). Cases of this kind are not infrequent when a very young root has been attacked by a moderate sized haustorium. It is usual in attacks on *Coleus*,

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* Leclerc du Sablon (Récherches sur les Organes d'Absorption des Plantes Parasites, Ann. d. Sc. Nat., Bot. Ser. VII, Vol. VI, pp. 90—117) asserts, with regard to *Melampyrum pratense*, that the secreting cells of the haustorium are unable to dissolve the lignified walls of the woody elements of the host's root. In *Thesium humifusum*, on the other hand, he definitely states that the woody cell walls are dissolved by the secretion.

Kusano (loc. cit.) states regarding *Buckleya Quadriala*, that while the wood of young roots is readily penetrated, it is exceptional for the sucker cells to penetrate mature wood and, even if this occur, it is only for a short distance along the medullary rays.

Peirce (loc. cit.) speaks of the haustorium of *Cuscuta americana* dissolving the woody cylinder "much more slowly." It seldom reaches the pith in *Mimosa*, sometimes in *Thevetia*.

Jatropha, Premna, Pupalia, Ruellia, and has been observed in several other cases.

Yet another form of penetration of the woody cylinder may be mentioned. In most of the tropical *Legumæinos* the strands of woody fibres in the central cylinder are concentrically arranged, this being a well-known character of the wood of this class of plants. The layers of xylem between these bands, being of a looser texture, are not infrequently penetrated by the sucker lobes. The edges of the lobes, having entered the xylem, are turned by the denser bands of fibres and pass sideways, just as they do between the sclerotic bands of the cortex. The outer parts of the woody cylinder then become thrust back by the swelling sucker lobes just as is the case with the wings of bark in ordinary penetration. An example of this kind of penetration is figured in *Acacia concinna* (Plate XIV, Fig. 1) where the phenomenon is of common occurrence. The general resemblance of such cases to compound haustoria is very striking, but a close examination shows that the doubling is internal only, and that there is only one pair of cortical folds. The haustorium is therefore simple outside but compound internally.

Of the other forms of penetration of the woody cylinder, that in monocotyledons alone need be mentioned. Here it is obvious that the sucker cannot develop lobes along the cambial line, and, once the protective sheath has been passed, the haustorium protrudes as a tongue-like process right through the cylinder, sometimes swelling up there into a hemispherical mass, and becomes attached to such bundles as it meets in its course.

The General Activity of the Haustorium.

16. It may be well in this place to note how very greatly sandal haustoria differ in their general activity. The haustoria found attached to various species of *Zizyphus* never seem to be well developed and, even after penetration, appear soon to die. In other cases, all is plain sailing and the whole of the host's root becomes flattened out before the advancing sucker.

The degree of activity in any haustorium will doubtless depend very largely upon the general health of the mother root, a factor which we are unfortunately unable to determine. An early connection of a young haustorium, again, is much more likely to be successful than when it has to wait for a long time before encountering a foreign root; for we have seen that the formation of haustoria does not depend on the presence of such roots in the soil. The maturity of the mother root and the stage of its development will doubtless have an important bearing on the subject, the amount of plastic substance available for carrying home the attack becoming rapidly less as the part advances in age, until, when the mother root at that part has become mainly a transmitting organ, little energy is likely to be available. On all these aspects of the case we have to confess ourselves entirely in the dark.

But, as will be seen below, the kind of root attacked appears to have a very definite influence on the activity displayed by the sucker. The smaller roots of many plants are as regularly penetrated as the older ones of the same species, but it is not surprising that, in many species, the smaller roots are fallen upon and broken up. Such have been observed in *Adenanthera Pavonina*, *Castanospermum australe*, *Coleus*, *Eucalyptus globulus* and in several others. In certain roots, notably *Cassia auriculata*, there appear to be no bounds to the energy of the haustorical attack. There appears to be no lack of protective appliances in the shape of sclerotic bands in this species, but in all the roots examined the fracturing action of the sucker is very marked. We have seen above (paragraph 14) that even the outside of the cortical wings are attacked in this species, and it would seem that the haustorial tissues are prepared to attempt an entrance at any part of these roots. A case in point is shown in Plate XV, Fig. 1. A reference to previous figures will show that, as a whole, the tissues of roots attacked remain in organic connection, so that, if all the sandal tissues were removed, the host's root would not fall to pieces. But in *Cassia auriculata* they are split up in the most extraordinary manner, little islands being formed in the transverse

section, around which active cells of the haustorium congregate, becoming granular and pouring out secretion. These fragments have been fallen on in their unprotected state, their cells have become discoloured and empty, and some of them are being completely dissolved. The sucker lobes in the figure are worthy of attention, for they have grown so actively that, after passing along the cambium and having cut off the wings of bark at their bases, they freely project (into the earth?) and their superficial cells are growing out like root hairs.

The reverse to the preceding is met with when we consider the many cases of dead or moribund haustoria which have been met with. The cause of this seems self-evident in such cases as *Zizyphus* where a general failure at penetrating to the wood has been noted, but it is less easy to understand what has happened in a series of haustoria collected on *Dalbergia scandens*. Every one of the twelve examined was quite dead. The fact is worth recording although no definite conclusion can be drawn for the following reasons. All the haustoria were taken in one locality and probably were connected to the same host, and all efforts at obtaining other examples have failed. Further, the sandal had succeeded in most cases not only in penetration but in fracturing the roots attacked. The remains of the dead haustoria were in every case cut off by well-formed layers of cork and so were all the tissues of the *Dalbergia* which had been injured. The *Dalbergia* roots were also in a very poor way, and it is possible that the sandal in its attack had actually cut off its own supplies. On the other hand, it is possible that the roots of *Dalbergia* have the power of emitting some injurious substance such as were met with in Peirce's experiments with roots which he forced to grow into various vegetable substances.*

Many dead or dying haustoria met with have succeeded in penetrating to the cambial layer. In some the root attacked was itself dead, but in the majority of cases it was apparently perfectly normal. We are thus led to the conclusion that

* Peirce, G. J. Das Eindringen von Wurzeln in Lebendigen Geweben. Bot. Zeit. 1894, I. Abth., pp. 169—176.

the death of the haustoria is usually due to their period of activity having passed. Perhaps the part of the mother root to which they belonged had ceased its absorptive work and merely become transmitting, the actually absorbing portion being pushed on to that part of the ground (usually along a hedge) where fresh roots were available. If the laborious operation of laying bare the sandal root-system is undertaken, many yards may be passed where the roots are thick and brown and the side roots are dried up and broken off. In one case carefully examined, a root was traced for 105 feet at an almost uniform depth of one to two feet in an almost direct line, without the discovery of a single living haustorium, although it is almost certain that, as this root advanced, it threw out its network of rootlets all covered with incipient haustoria. From the examination of this and a number of other sandal root-systems in connection with another piece of work, taken together with the frequent occurrence of dying haustoria on healthy young roots, the general idea which forces itself upon one is that there is a gradual extension of the active part of the parasitic root-system, so that in some cases the place to search the ground for the living haustoria of a well-grown tree may be many yards away from its trunk.

When the haustorium has died and its tissues have crumpled away, it leaves a characteristic scar. These can be noted in quantities on all the older roots near the trunk. Such a scar is shown in Plate XIV, Fig. 2, and it is interesting to note that in this case the attacked root has not developed any corky covering to its exposed xylem ; there is no attempt at occlusion, but the necessary protection is afforded by the tissues killed and filled with dark brown gummy substance.

The Inter-relations of Host and Parasite.

17. In concluding this study of the structure of the haustorium of the sandal, I propose to summarize the result obtained regarding the inter-relations of host and parasite.

We have seen that the energy of the attack and the ease with which penetration is effected vary a good deal—vary from a

comparative harmlessness to an almost ferocious activity. The root attacked is by no means passive under these onslaughts. The study of the mutual influence of host and parasite is a large one. The mere cataloguing of the various means adopted by various species to protect themselves would be a considerable piece of work, but a full study could not well be carried through without a similar study of the effects of ordinary wounds upon the tissues. It is hoped that at some future time such a study may be undertaken, but it should include the other haustoria of this type. Here some of the most striking cases may be noted from the series of observations already made during the course of the present investigation. A somewhat more difficult problem presents itself when we consider the influence exerted upon the tissues of the haustorium by the root attacked. We have repeatedly met with indications that the haustoria attacking certain roots usually develop certain tissues more than others, but the influence thus suggested of host on parasite will require very careful verification before the matter can be considered definitely settled. It so frequently happens that the sections obtained through haustoria on a certain host have all been collected in one place. It is only by collecting and comparing such sections from widely separated regions and by carefully studying the local conditions that any positive statements can be made.

When a sandal haustorium makes its attack upon a foreign root and attempts to effect an entrance, it relies chiefly upon the pressure it is able to exert and the solvent action of its secretions. The pressure is to all appearance caused by its rapid growth in the soil, on the one hand being closely applied to the host's root, and on the other being surrounded by the dense masses of soil. Indications of this pressure are not wanting. The root attacked is sometimes altered in shape. This has been noticed especially in the roots of *Cansjera Rheedii*, (garden) *Coleus*, (garden) *Acalypha*, *Guazuma tomentosa*, *Pterolobium indicum*, *Sarcostemma brevistigma*, *Tecoma Stans* and *Santalum album*, the roots in some of these having been very distinctly flattened or nipped by the haustorial pressure. When the bark of the root has been

ruptured, a tongue-like protrusion of the sucker is thrust into the fissure. The process then grows greatly in size, exerting pressure in all directions, since the whole complex is held firmly in position by the cortical folds. The wings of the bark are thrown widely apart in almost all cases, and in *Gyrocarpus Jacquini* and *Jatropha gossypifolia* these wings have been seen considerably squeezed and greatly reduced in thickness. Opposite the place of contact between the sucker and the woody cylinder, the cells are occasionally squashed and flattened. In *Gyrocarpus Jacquini* and *Jatropha gossypifolia* the woody cylinder as a whole has been considerably flattened, while in *Acacia Cæsia*, *Ficus mysorensis*, *Ficus religiosa*, *Grewia tiliæfolia*, *Gyrocarpus Jacquini*, *Jatropha gossypifolia* and *Pithecolobium dulce* individual vessels have been noted whose lumen has been completely closed by the pressure. Lastly, as has already been pointed out in *Gyrocarpus Jacquini*, the ends of the vessels of the haustorium have been seen to be thrust into the vascular cavity, a further evidence of pressure.

The sucker secretes at all parts of its surface, wherever it meets the host's tissues. This occurs along the general surface of the woody cylinder, but especially at the end of the growing lobes. In some cases a special gland is formed, charged with mucilaginous substance. This secretion sometimes acts at a considerable distance, apparently unharmed tissues intervening. A number of cases have been noted where the action of the secretion has been detected some distance inwards before any opening has been effected. This is usually shown by the filling of the vessels with gummy substances or thyloses, the darkening of the parenchyma or the medullary rays and, more frequently, by the discoloration of the fibrous bands of sclerenchyma. Such distant action has been noted in *Alangium Lamarckii*, *Albizzia amara*, *Cassia auriculata*, *Cordia Myxa*, *Dodonæa viscosa*, *Kigelia pinnata*, *Melia azidarachta*, *Peltophorum ferrugineum*, *Pterolobium indicum* and *Zizyphus Oenoplia*.

With these resources at its command, the general course of the haustorial action varies a good deal, and this does not altogether depend, to all appearance, on the resistance to be expected

from the tissues opposed to it. When a small root is met with, not unnaturally the action is often energetic and the root is more or less devoured. Such cases have been noted in *Adenanthera Pavonina*, *Castanospermum australe*, *Casuarina equisetifolia*, (garden) *Coleus*, *Eucalyptus Globulus*, *Kigelia pinnata*, *Peltophorum ferrugineum*, *Santalum album* and *Tamarindus indica*.

In attacks on certain roots, as has been remarked, there appears to be special activity. Such are *Cassia auriculata*, where the growth of the sucker lobes is so great that they come out on the other side of the root attacked. In this species and in *Opuntia Dillenii* the result is the general breaking up of the root, as also is the case with the soft roots of species of *Ficus*.

On the other hand, there appears to be successful resistance to penetration, as in *Ochlandra Rheedii* and probably many monocotyledons. The haustorium seems to have poor chances of effectively entering roots of *Zizyphus* species, and perhaps this is the case with *Asparagus racemosus* where a firm band of sclerotic tissue is formed outside the vascular cylinder.

Dead or moribund haustoria have been found on some 23 species of plants. But it cannot be therefore concluded that the sandal has been worsted in the conflict. Many of these dead haustoria are seen to have successfully penetrated and grown for some distance along the cambial line, and probably many are in a bad state of health because of the condition of the root of the sandal to which they belong. Obviously nothing can be certainly deduced from the death of the haustoria without a knowledge of the state of the whole system to which they belong. And even where, as in the case of *Dalbergia scandens*, all the sandal haustoria were dead, this may have been caused by some local accident.

Cases have been noted where failure to penetrate has been due to the tendency of the sucker lobe to pass along the line of least resistance, where it has been, so to speak, misled and wandered aimlessly between cortical layers of fibrous cells. Many such lobes have been found dried up and dead.

In conclusion, two cases of exceptional interest may be here noted. In sections of sandal haustoria attached to the roots of

Jasminum it is sometimes extremely difficult to draw the line between the cells of the haustorium and host. There is in almost all other cases the sharpest line of demarcation, generally accentuated by a layer of gummy substance. Whether actual fusion of tissues occurs here or not, this seems to be the case in certain sections through haustoria which have become fixed to the roots of *Sandal* itself. That such fusions should occur would appear more or less natural.

On the other hand, most self-attacks show a very remarkable effort at resistance on the part of the *Sandal* root attacked. So great is this that there is every reason to suppose that a very well defined attempt is being made to throttle the sucker, the appearance being that of a tissue defending itself by occluding the wound made. This has been already referred to and is illustrated in Plate XVI, Figs. 1 and 2.

18. The resistance offered by the host's tissues to the sucker's progress is very various, depending as it must do mainly on the amount of living force in the different tissues and, as will be seen, especially in the cortex.

There is the natural resistance of the tissues against destruction. Such are the corky layers which are sometimes so dense that the haustorium seems unable to effect an entrance. The sclerotic bands again not infrequently bar its progress, while in most cases it is able to make little impression on the vascular cylinder. Parenchymatous tissue, on the other hand, wherever met, is almost universally easily and quickly disintegrated by its secretions.

New growths are sometimes formed before the sucker has succeeded in getting at the wood, in some cases indeed before any penetration has been effected. Thus in *Alangium Lamarckii* a case has been noted where an extra corky layer has been placed opposite the point of contact of the haustorium and the root. This has been also noted in *Ficus mysorensis*. In *Melia Azidarachta* the cambium in one section is growing in curious excess opposite the point where the haustorium has applied itself,

while in *Sarcostemma brevistigmo* new thick layers of sclerenchyma are formed in the cortex before any of the outer tissues have been ruptured.

When the sucker has broken through the corky layers of the bark, but before it has reached the wood, protective layers are sometimes formed in the cortex, usually of the nature of cork.* It is not certain in all cases that the sucker has not given up growing, and the formation of cork would be natural in such cases. It appears, however, that in monocotyledons the cortex is specially fitted for this cork formation. It has been noted in *Sansevieria zeylanica*, *Phoenix dactylifera*, and *Agava Vera-Cruz* that the tongue-like sucker is cut off from the cortex by a well defined layer of cork before the vascular system has been reached. This has also been met with in *Albizzia Amara* and *Guazuma tomentosa*, while in *Zizyphus rugosus* and *Z. Oenoplia* the cork has been formed to all appearance after the sucker has been definitely defeated and has ceased to grow. In *Panax* (garden) the whole end of the sucker is bounded by a layer of cork, although it has succeeded in forcing its way deep into the soft woody cylinder. In *Dalbergia scandens* all and every trace of the haustoria is carefully cut off by such layers, but here all are dead and disintegrated.

After the woody cylinder of the host has been reached, cork is not infrequently developed on each side of the cortex where it comes into contact with the sucker. The layer of cork then forms an inner lining to the two wings of bark which have been more or less widely thrust apart. This has been noted in *Acacia Caesia*, *Capparis zeylanica*, *Clausena indica*, *Ficus religiosa*, *Grewia tiliæfolia*, *Jatropha gossypifolia*, *Melia Azidarachta*, *Parkia biglandulosa*, *Pithecolobium dulce*, *Pongamia glabra* and *Pupalia atropurpurea*.

Such layers of cork are formed in certain species, not only on the inner side of the cortex but right through its thickness, with the result that the wings are completely cut off by a band

* Hartig terms this cork formed by the cortical cells as protection against parasitic attack "wound cork." (Diseases of Trees, Sect. II., Wounds.)

of cork at their base. This has been noted in *Casuarina equisetifolia*, *Pterolobium indicum*, and *Tecoma Stans*, while it has been partially cut off in sections of *Grewia tiliæfolia* and *G. hirsuta*.

A further secondary growth in the wings of bark is met with in certain plants. The tissue formed is various in structure, but, from the frequent occurrence of vascular elements, it has the general appearance of wood. Its formation depends presumably on the amount of vitality retained by the cortical cells, and much light would be thrown on the subject by the study of wounds and their healing tissues. Thus in *Acalypha indica*, rounded masses of cells are to be met with in the wings after they are thrust aside. So in *Capparis zeylanica* and *Lantana Camara*. In *Cansjera Rheedii* there is a considerable merismatic growth along the inner sides of the wings. Finally, in *Santalum album* great masses of tissue including vessels in regular rows have been met with in ten different roots, indicating that the secondary growth in the cortex is the rule (Plate XVI).

19. But these growths in the cortex are insignificant when compared with what takes place opposite the ends of the sucker lobes. Here the haustorial secretive cells are most active, and here lies the actively growing part of the root attacked, the cambium. The tissues formed at this point vary greatly in different species and require very careful study to determine whence they arise. The cells are corky, lignified or cellulose parenchyma, or more or less altered wood. Details are not possible in this place.

What appear to be corky wedges are seen in *Acacia concinna*, *Blepharis boerhaaviæfolia*, *Capparis zeylanica*, *Casuarina equisetifolia*, *Grewia tiliæfolia*, *Guazuma tomentosa*, *Pterolobium indicum*, *Jatropha gossypifolia*, *Lantana Camara*, *Pongamia glabra*, *Premna tomentosa* and *Santalum album* (one doubtful case). These corky layers may arise to all appearance from cambium or from cortex. In *Tecoma Stans* there are two layers distinguishable, and these probably arise from cambial and cortical mother cells respectively.

Not infrequently small wedges of xylem are thrust forward opposite the ends of the sucker lobes. The structure of these

requires further study, for they sometimes differ very markedly from the ordinary woody tissue of the root. Such have been noted in *Acalypha indica*, *Blepharis boerhaaviæfolia*, *Guazuma tomentosa*, *Pithecolobium dulce* (Plate XIV, Fig. 2), *Premna tomentosa*, and markedly in *Santalum album* (Plate XVI, Fig. 1). In *Ficus mysorensis* a great development of woody parenchyma is seen opposite the angle of attack, while in *Casuarina equisetifolia* a mass of thick-walled parenchyma grows outwards along the inner side of the wing. A similar growth has been noted in one case of *Lantana Camara*.*

The extrusion of "gum" is universal where the haustorium comes in contact with the host's tissues.† This is a well-known protection of woody tissues against attack by wounding or parasite, and is best seen along the surface of the woody cylinder. It is found all along the line of contact with the sucker and fills the lumina of the neighbouring cells and vessels, but is most abundant in the angle formed by the cylinder and cortical wing, occupied by the lobe of the sucker.‡

The gum is generally a clear yellow as in *Citrus Aurantium*, but in many cases assumes a darker colour, the browning of tissues being very marked, as in *Grewia*. Sometimes it takes on specially brilliant colours, all shades of reds and browns being found in *Cassia auriculata*, and deep black in *Capparis zeylanica* and *Diospyros montana*.

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* This formation of woody wedges opposite to the end of the sucker lobes should be studied in relation to the wound wood formed on exposed wood surfaces and "callus wood" formed after wounds. As Hartig points out, the structure of such wood differs considerably from that of the ordinary woody cylinder, and it would be interesting to compare the woody wedges formed after an attack of a haustorium sucker with that formed after wounds in the same roots.

† Strasburger, Leitungsbahnen, pp. 771—3. Protective gum and thyloses are quickly formed to stop the vessel cavities in wounded roots.

‡ An altogether similar gummy layer between the sucker and the host's tissues is described as follows by Solms Laubach for *Thesium* :—The whole sucking process lies with its sucking apex in the wood and is separated both from the wood and cortex by an irregular layer of homogeneous yellow, strongly refractive substance.....The function of the yellow mass in the angle of attack at the end of the sucker lobe is the separation of the cells of the host and parasite.

While the vessels and parenchyma become filled with this brown substance, the sclerotic bands become markedly discoloured in their cell-walls, and sometimes these colourings are also brilliant in the extreme. As might be expected, such colorations are chiefly met with in the *Leguminous* plants, and *Acacia concinna*, *Albizzia amara*, *Pithecolobium dulce* and *Pongamia glabra* may be taken as typical examples.

Thyloses are present in certain species, with or without the occurrence of gum. They are usually to be met with in the woody cylinder opposite to the sucker, but in some cases the whole of the section is thus filled. They have been marked in *Casuarina equisetifolia*, (garden) *Coleus*, *Cordia Myxa*, *Ficus religiosa*, *Ficus mysorensis*, *Gyrocarpus Jacquini*, *Jatropha gossypifolia*, *Jatropha Curcas*, *Pithecolobium dulce*, *Pterolobium indicum*, *Santalum album*, *Tecoma Stans* and *Thespesia populnea*, and a further search would doubtless show their presence in other species. Perhaps they would then prove to be typically present in certain orders as was noted by Molisch.*

The curious case of *Gyrocarpus Jacquini* has been already mentioned where the endings of the haustorial vessels appear to form the thyloses in vessels near the place of contact, the latter assuming the reticulated markings of such vessels.

It is frequently to be noted that the discoloration of the tissues of the host's root, whether by the formation of gum in the vessels, browning of the parenchyma, the formation of thyloses or the colouring of the bands of woody fibres, is closely related to the surface of contact with the sucker, so to speak imaging the area through which its influence is felt. On the one hand, it may be regarded as an attempt to block the path of injury or of fluids, and on the other, it shows the destructive effects of the haustorial action on the host's tissues. Not infrequently the zone of discoloured tissue corresponds very exactly with the part between the two ends of the lobes; sometimes this zone is more

* Molisch, Zur Kenntniss der Thyllen nebst Beobachtungen über Wund-heilung in de Pflanze, Sitzb. d. Wien. Akad. d. Wiss., Bd. XCVII, I Abth., 1888, p. 285.

or less superficial, while in other cases a wedge of discoloration passes right to the centre of the cylinder. Such wedges are very striking in the sections and demonstrate at once, were proof needed, that the sucker is the sole cause of the death in the parts marked out. As cases in point, the figures on Plate XIV may be noted, the area of injury being generally darker in colour.

In a few cases, lastly, a curious thin brown line is met with, which separates the discoloured tissues from the normal ones. This has been noted in *Pithecolobium dulce*, *Pithecolobium Saman* and *Pterospermum indicum*. It has no structural character, but is merely a darkening of the tissues along the separating line.

Secondary thickening in the host's root after penetration has been effected is by no means uncommon, even in such cases as that figured on Plate XV, where a root of *Cassia auriculata* has been shattered completely. In most cases, however, the secondary thickening is seen to follow the more or less successful barring of the further progress of the sucker lobes, thus freeing the cambium for further growth. Such thickening has been noted in the following species:—*Acacia Cæsia*, *Acalypha indica*, *Blepharis boerhaaviæfolia*, *Cassia auriculata*, *Casuarina equisetifolia*, *Grewia tiliæfolia*, *Guazuma tomentosa*, *Jasminum rigidum*, *Jatropha gossypifolia*, *Lantana Camara*, *Opuntia Dillenii*, *Parkia biglandulosa*, *Pithecolobium dulce*, *Pithecolobium Saman*, *Polyalthia longifolia*, *Pongamia glabra*, *Premna tomentosa*, *Pterolobium indicum*, *Ruellia prostrata*, *Santalum album*, *Tecoma Stans* and *Toddalea aculeata*. This list would in all probability be greatly increased if more sections were cut of the material collected. There seems to be no reason why almost every root should not thus go on growing after the attack has been driven home. In the great majority of cases the growth of tissues opposite the ends of the sucker lobes is sufficient to prevent the further progress of the parasite, and the cambium is thus free to go on dividing as usual.

July, 1906.

APPENDIX I.

LIST OF SANDAL HOSTS.

(* Sections cut and examined.)

* Acacia cæsia.
* „ concinna.
* Acalypha (garden).
* „ indica.
fruticosa.
Achyranthes aspera.
* Adenanthera pavonina.
Adhatoda vasica.
* Agave Vera-Cruz.
* Ailanthus excelsa.
* Alangium Lamarckii.
* Albizzia amara.
Alseodaphne semicarpifolia.
Anona squamosa.
Arenga saccharifera.
* Artabotrys odoratissimus.
* Asparagus racemosus.
Azima tetracantha.

Bambusa auriculata.
* Berrya ammomilla.
* Begonia (garden).
* Blepharis boerhaaviæfolia.
* Cansjera Rheedii.
* Capparis zeylanica.
Caryota sobolifera.
„ urens.
Casearia tomentosa.
* Cassia auriculata.
* „ siamea.
* Castanospermum australe.
* Casuarina equisetifolia.
* Celastrus paniculata.
Cipadessa fruticosa.
* Citrus Aurantium.
* Clausena indica.
Clitoria Ternatea.
* Cocos nucifera.
* Codiæum (garden).
* Coleus (garden).
* Combretum ovalifolium.
* Cordia Myxa.
Cucurbita dioica.
Cudrania javanensis.
Cynodon dactylon.
* Cyperus rotundus.

* Of the sandal hosts on which haustoria were cut and examined under the microscope, 53 were collected in the typical Mysore sandal zone, 26 were kindly contributed by Mr. Rama Row of the Madras Forest Department, 10 were collected in hedge rows in Madras city, and a number were reared in pots. In many cases the same plant was collected in two or more of these classes.

* Dalbergia scandens.
„ Sissoo.
* Diospyros montana.
* Dodonæa viscosa.
* Dolichos Lablab.
* Dracæna (garden).

Elæodendron Roxburghii.
Eleusine ægyptiaca.
* Eucalyptus globulus.

Ficus bengalensis.
* „ mysorensis
* „ religiosa.
* Flueggea leucopyrus.

* Grewia hirsuta.
* „ tiliæfolia.

* Guazuma tomentosa.
* Gymnosporia montana.
* Gyrocarpus Jacquini.

Heptapleurum verticillatum.
„ venulosum.
* Holoptelea integrifolia.

* Jasminum malabaricum.
* „ rigidum.
* Jatropha Curcas.
* „ gossypifolia.
* Kigelia pinnata.

* Lantana Camara.
* Leucena glauca.
Limonia acidissima.
Litsæa zeylanica.

* Melia Azadirachta.
* Meyena (garden).
Mimusops indica.
Morinda citrifolia.

* Ochlandra Rheedii.
* Opuntia Dillenii.

* Panax (garden).
* Parkia biglandulosa.
* Pavetta indica.
* Peltophorum ferrugineum.
* Phœnix sylvestris.
* Pithecolobium dulce.
* „ Saman.
Plumbago zeylanica.
* Polyalthia longifolia.
* Pongamia glabra.
* Premna tomentosa.
* Protium caudatum.
* Psidium Guyava.
* Pterospermum Heyneanum.
* Pterolobium indicum.
* Pterospermum suberifolium.
* Pupalia atropurpurea.

* Ruellia prostrata.

Saccharum spontaneum.
* Sansevieria zeylanica.
* Santalum album.
* Sarcostemma brevistigma.
Sida carpinifolia.
* Sida rhombifolia.
* Stachytarpheta indica.
* Sterculia alata.
Sreblus asper.
Strobilanthes cuspidatus.

* Tamarindus indica.
* Tecoma Stans.
* Terminalia Arjuna.
* „ Chebula.
* Thespesia populnea.
Tinospora cordifolia.
* Toddalia aculeata.

Ventilago madraspatana.

Webera asiatica.
Wrightia tomentosa.

* Zizyphus Œnoplia.
* „ rugosus.
„ xylopyrus.

APPENDIX II.

SOME TYPICAL PLANTS OF THE TRUE SANDAL ZONE IN MYSORE.*

Acacia Catechu.
,, concinna.
,, ferruginea.
Alangium Lamarckii.
Albizzia amara.
,, odoratissima.
Anamirta cocculus.
Anogeissus latifolia.
Asparagus racemosus.
Atalantia monophylla.

Balanites Roxburghii.
Bassia longifolia
Bauhinia racemosa.
Boswellia serrata.
Boucerosia umbellata.
Bridelia retusa.
Buchanania latifolia.
Butea frondosa.

Cadaba indica.
Canthium didymum.
Cansjera Rheedii.
Capparis divaricata.
,, horrida.
,, sepiaria.
Cardiospermum Halicacabum.
Careya arborea.
Carissa spinarum.
Cassia auriculata.
,, Fistula.
Celastrus paniculata.
Chloroxylon Swietenia.
Cocculus villosus.
Cochlospermum Gossypium.
Cordia Myxa.

Diospyros montana.
,, Tupru.
Dodonæa viscosa.

Erythrina stricta.
Eugenia Jambolana.
Feronia Elephantum.

Gmelina asiatica.
Grewia humilis.
,, tiliæfoliā.
Gymnosporia montana.

Hiptage Madnablota.
Holoptelea integrifolia.

Ixora parviflora.

* Collected and determined by my assistant, Mr. C. Tadulingam. The expedition was however unfortunate in that, because of an unusually dry season, few plants were in flower and the bulk had to be determined without this aid

Jasminum malabaricum.
Jatropha Curcas.

Lagerstrœmia lanceolata.
Lantana Camara.
Lawsonia alba.

Morinda citrifolia.

Parkinsonia aculeata.
Plumbago zeylanica.
Pongamia glabra.
Premna tomentosa.
Protium caudatum.
Psidium Guyava.
Pterocarpus Marsupium.
Pterolobium indicum.

Schleichera trijuga.
Soymida febrifuga.

Stachytarpheta indica.
Stephegyne parvifolia.
Stereospermum chelonoides.
Streblus asper.

Terminalia belerica.
,, paniculata.
,, tomentosa.
Toddalia aculeata.
Trema orientalis.

Ventilago madraspatana.
Vitex altissima.
Vitis pedata.

Wrightia tinctoria.

Zizyphus Jujuba.
,, Oenoplia.
,, rugosa.

DESCRIPTION OF FIGURES.

PLATE I.—

A sandal haustorium which has successfully penetrated a root of *Alangium Lamarckii*. The tissues are still quite young and vessels are only formed in the upper part; *a*, upper part of the nucleus; *b*, lower, elongated part of the nucleus; *c*, parenchyma of the transitional region; *d*, parenchyma of the outer cortex already becoming permanent; *e*, parenchyma of the inner cortex; *f*, edge of sucker lobe adjoining the woody cylinder of the host.

PLATE II.—

Fig. 1. A young haustorium which has entered a root of *Sida rhombifolia*. The tissues of the haustorium have reached a further stage in development than in plate I, and a strand of vessels has appeared on each side of the nucleus where it joins the cortex. Letters as in the last plate, *vv*, vessels. In the middle line of the sucker a small slit shows the remains of an old gland, *gl*.

Fig. 2. A part of the cortex of *Grewia tiliæfolia* in contact with the epithelial cells of the sucker (as in Plate XI, Fig. 2). The cell walls are almost dissolved away and the large starch grains fill the field. Note the effect of the secretion of the epithelial cells upon the strands of sclerotic cells, *scl*; *st*, starch grains; *ep*, sucker cells.

PLATE III.—

A mature haustorium which has penetrated a root of *Citrus Aurantium*. The tissues of the haustorium may be compared with those in the two previous plates, the letters referring to the same tissues here in an older stage of growth; *iz*, interrupted zone of the vascular system.

PLATE IV.—

A set of diagrammatic figures showing sections through a mature haustorium cut in various directions.

No. 1. Diagrammatic view of a haustorium cut in half. The smaller figures indicate the planes in which Nos. 3 and 4 are cut.

No. 2. View of the transverse section seen at the cut surface exposed in No. 1. The smaller figures show the planes in which Nos. 6—10 are cut. The diagram is of a mature haustorium which has successfully penetrated a dicotyledon root; *m*, mother root; *tr*, transitional region; *cf*, cortical fold; *cl*, collapsed layer; *ic*, inner cortex; *n*, nucleus; *vv*, vessels; *sl*, sucker lobe; *b*, bark and *w*, wood of the host's root.

Nos. 3 & 4. Transverse sections through the planes marked 3 and 4 in diagram 1.

No. 5. Transverse section through a young haustorium, not yet penetrated, with a glandular slit, *gl*, in the middle of the nucleus.

Nos. 6—10. Horizontal sections through the planes marked 6—10 in diagram 2, the lettering being the same in all cases.

No. 11. Vertical section through diagram 2 a little on one side of the median line.

PLATE V.—

Fig. 1. A sandal haustorium attacking a root of *Pithecolobium dulce*. Note especially the meristematic development, *me*, in the outer cortex immediately outside the collapsed layer on either side. A well-defined layer of cork, *ck*, is seen outside the haustorium. The lacunar tissue inside the collapsed layers is well seen.

Figs. 2 & 2^1. A young haustorium endeavouring to enter a root of *Albizzia amara*. The cortical folds are thrown into convolutions and in one place a piece of the host's bark, *bk*, is being rolled back like a carpet, showing the shearing action of the cortical fold.

Fig. 3. A sandal haustorium attacking a young root of *Gyrocarpus Jacquini*. The sucker is broad and has forced its way right across the width of the root to a considerable depth, flattening the vascular cylinder and compressing some of its vessels. Meantime the cortical folds are burrowing into the outer, loose corky layers.

Fig. 4. A small portion of a section through another haustorium also fixed on *Gyrocarpus Jacquini*. In two places the vessels of the sucker have to all appearance penetrated the vessels of the host as thyloses, *th*, and the latter have assumed the usual reticulations of the sandal vessels.

PLATE VI.—

Figs. 1 & 2. Sections cutting through a haustorium fixed on *Citrus Aurantium* in different horizontal planes, to illustrate the changes taking place in the vascular system. The upper section is through the transitional region and the lower through the interrupted zone; *cl*, collapsed layers.

PLATE VII.—

Figs. 1 & 2. Horizontal sections through a haustorium fixed on *Clausena indica*, showing the vascular system from the interrupted zone to the axial region of the nucleus, *n* ; *cl*, collapsed layers ; *ck*, cork.

PLATE VIII.—

Horizontal section through the axial region of the nucleus in a haustorium fixed on *Thespesia populnea* ; *cl*, collapsed layers ; *ic*, inner meristem; *oc*, outer meristem or cambium ; cl^1, collapsed layer down the middle of the nucleus.

PLATE IX.—

Transverse section through a haustorium fixed on *Pithecolobium dulce*, showing marked secondary thickening ; *cl*, collapsed layer ; *iz*, interrupted zone ; *me*, meristem in the outer cortex ; *ck*, cork ; *scl*, discoloured bands of sclerotic cells.

PLATE X.—

Fig 1. The end of the lobe of a sucker fixed on a root of *Casuarina equisetifolia*, showing the formation of vessels and the effect of the secretion upon the cortical cells of the host. A vessel has been squeezed flat at one part of the section.

Fig. 2. A section through the end of a young lobe of a sucker attached to the root of *Cordia Myxa*. The cells of the sucker are protoplasmic and actively dividing, and a clearly marked layer of glandular cells is seen as a sort of secreting epithelium. The structure of these cells appears to be identical with that of the cells of the gland (Part I, Plate V, Fig. 23). Note the effect of the secretion upon the cells of the host.

Fig. 3. Another part of the same section where the cells of the sucker are opposite the cells of the woody cylinder and presumably in an older stage of development. Note the effect of the secretion as before.

PLATE XI.—

Fig. 1. Section through a haustorial attack on a root of *Pterolobium indicum*. One lobe of the sucker has reached the woody cylinder and passed along the cambial line. The other has, however, only succeeded in piercing part of the cortex and is wandering aimlessly in this tissue. Various parts of the host's tissues show by their discoloration the effect of the parasitic secretions, while several layers of cork have appeared in the cortex on one side.

Fig. 2. Section through a haustorium fixed on a root of *Grewia tiliæfolia*. The cortex has been irregularly torn by the sucker, isolated masses being attacked by the adjoining cells of the parasite (cf. Plate II, Fig. 2). A layer of protective cork has been formed right round each of the wings of the host's bark.

PLATE XII.—

Fig. 1. In *Diospyros montana* the effect of the sucker at a distance is seen in the dense black coloration of the host's tissues. The wings of bark are cut off at the base. The lateral or tangential working of the secretion, as shown by the ring of wood cut off, may be explained by the structure of the ebony wood which is characterized by tangential rows of thin-walled parenchyma.

Fig. 2. In *Ficus mysorensis* the soft woody cylinder is irregularly ruptured, lobes not being formed by the sucker which protrudes as a blunt process right into the root.

PLATE XIII.—

Fig. 1. In *Opuntia Dillenii* the sucker breaks up irregularly, taking advantage of the broad medullary rays to penetrate the soft woody cylinder. One of the processes of the sucker has passed right through the pith and has nearly reached the cortex on the other side.

Fig. 2. In *Jatropha gossypifolia* the tissues of whose root are soft all through, the sucker forms a broad turgid mass and bores its way right across the root, flattening out the woody cylinder before it in its progress. A well-marked layer of cork is formed at the base of each wing and curves round to protect the cambium from the effect of the sucker's action.

PLATE XIV.—

Fig. 1. In *Acacia concinna* the sucker has penetrated the woody cylinder, and its lobes are passing between the concentrically arranged bands of sclerotic cells. The result is curious, in that, *internally*, the haustorium is compound, with two well developed sets of collapsed layers, while, *externally*, it is simple and has but one pair of cortical folds.

Fig. 2. The "scar" left by an old, dead haustorium on a root of *Pithecolobium dulce*. The wings of cortex are dead and have been cut off by corky layers from the still living part of the cortex. The haustorial tissues are completely decomposed and are represented by mere shreds of dead cells adjoining the woody cylinder. The effect of the sucker's action is well marked and

the area of its influence is seen by the discoloured (dark brown) sclerotic bands and the vessels filled with dark gummy masses. Secondary thickening has commenced, but the wood formed after attack is distinguished by the smallness of its vessels and its general uniform, small-celled character.

PLATE XV.—

Fig. 1. In *Cassia auriculata* the attack of the haustorium is seen to be very energetic. The woody cylinder has been almost surrounded by the sucker lobes which have cut off the wings of cortex and separated them completely from the body of the root. The woody cylinder shows the effect of the parasitic action in the discoloration of the sclerotic layers and the vessels filled with black, gummy substance. The sucker lobes, still full of activity, have passed right through the root and are producing root-hair-like outgrowths at their free surfaces, while the small, uninjured part of the host's cambium is forming a small subsidiary woody mass, plentifully surrounded by corky layers.

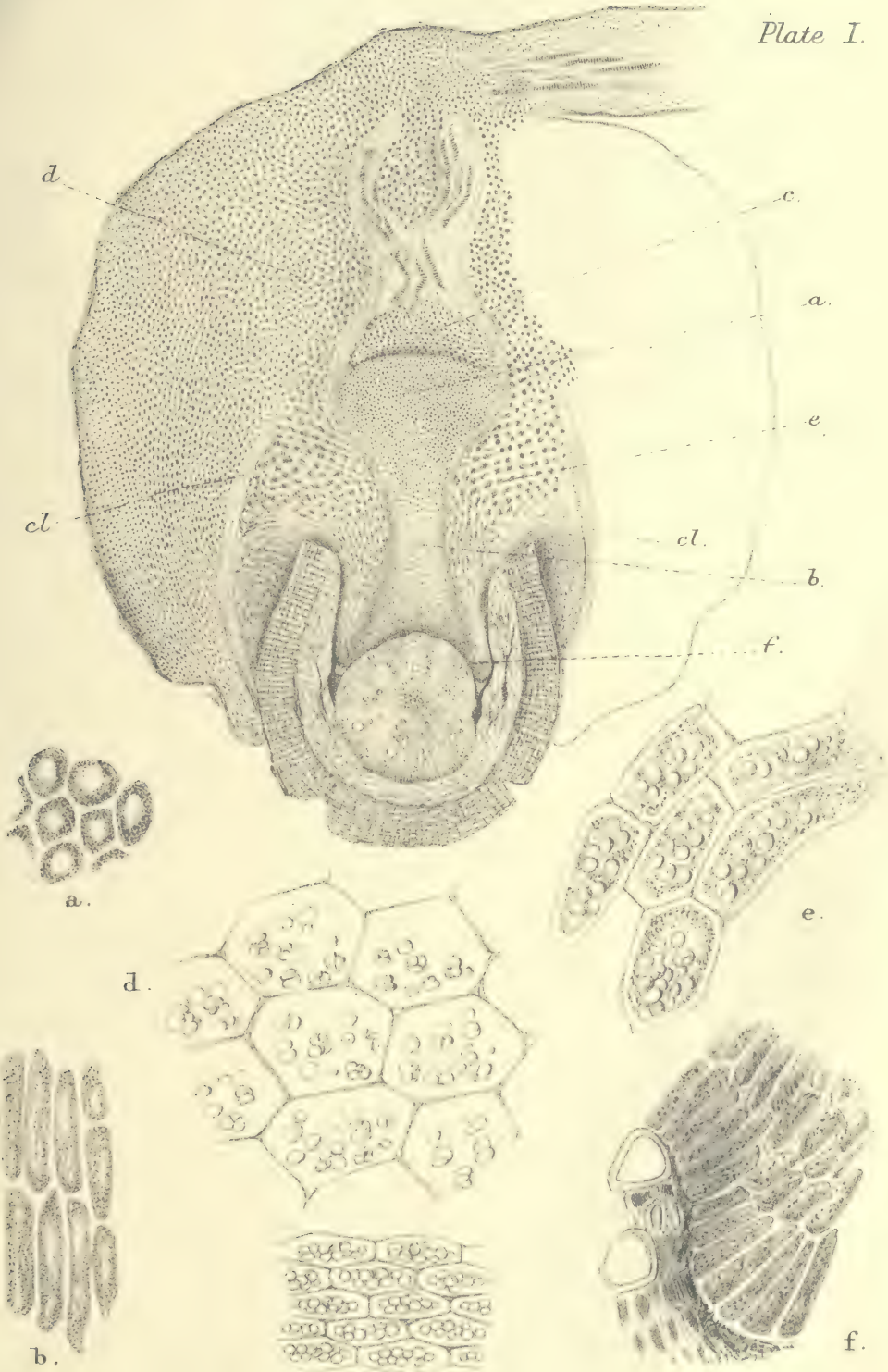
Fig. 2. A small portion of the above section at *a* magnified to show the vascular structure in "transverse" section ; *mr*, medullary ray ; *v*, vessels of secondary wood; *camb*, cambium ; *ic*, inner cortex becoming collapsed.

PLATE XVI.—

Fig. 1 A sandal haustorium fixed upon a sandal root. A great meristematic growth, *me*, is taking place in the cortex of the attacked root on each side of the sucker, the result of which is the gradual occlusion of the wound. The haustorium is apparently moribund. Note the small woody wedge, *a*, formed opposite the end of the sucker lobe and barring its further progress. *v*, vessels, &c.

Fig. 2. A young stage of the above case, showing the commencement of the meristem on the inner side of the cortical wing ; *me*, secondary cortex ; *v*, vascular elements ; *cl*, collapsed layers ; *sl*, sucker lobe.

Plate I.



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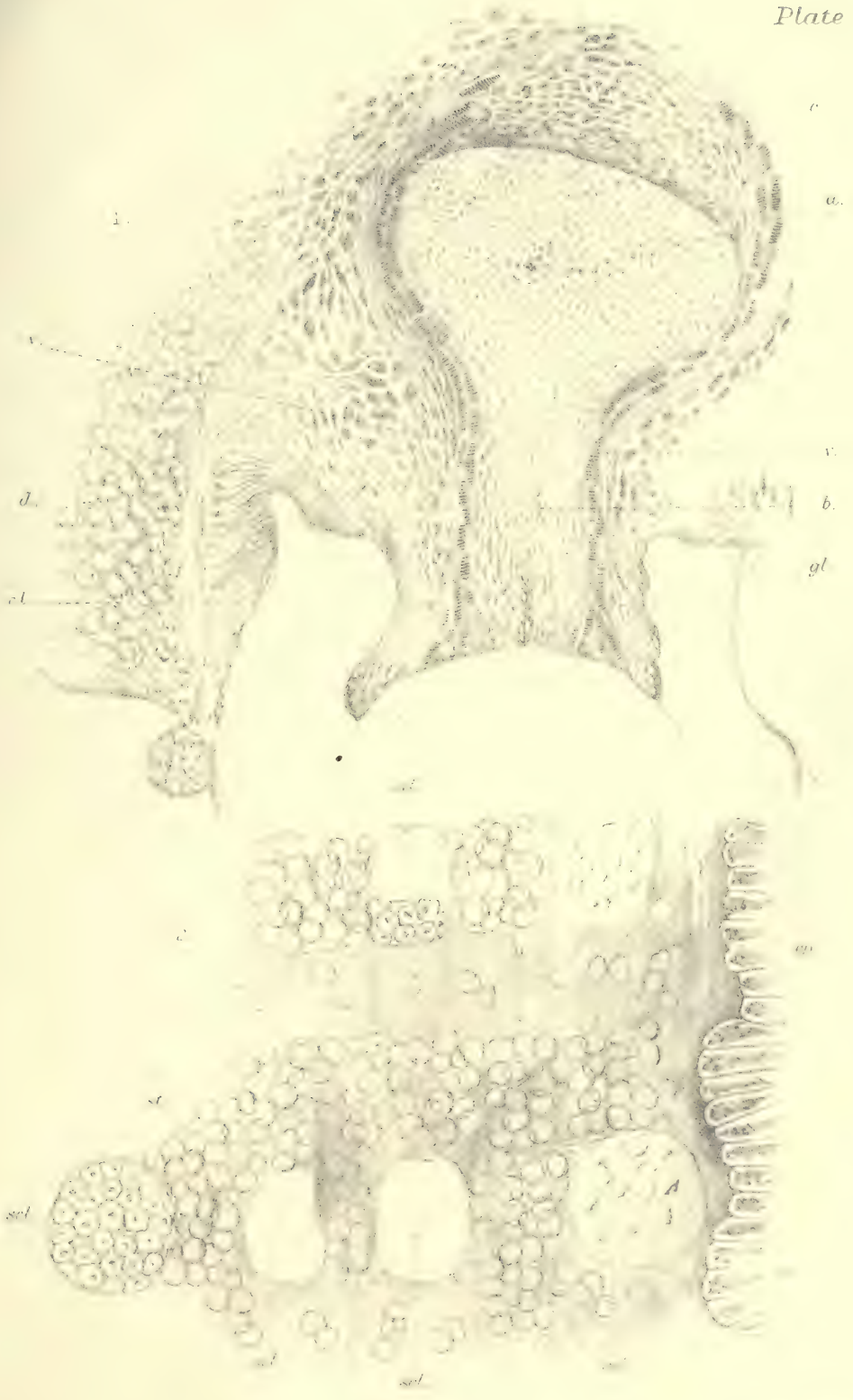
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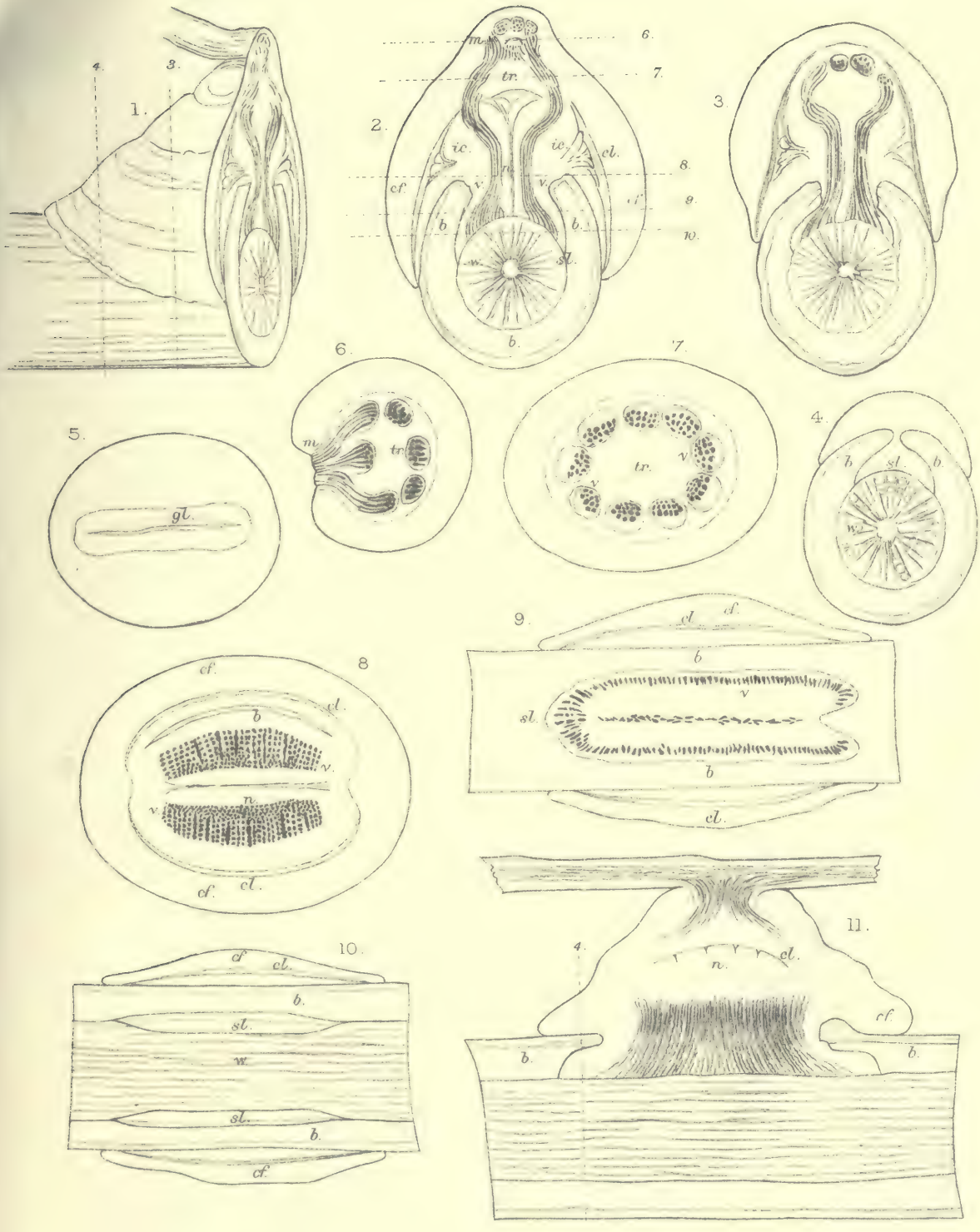

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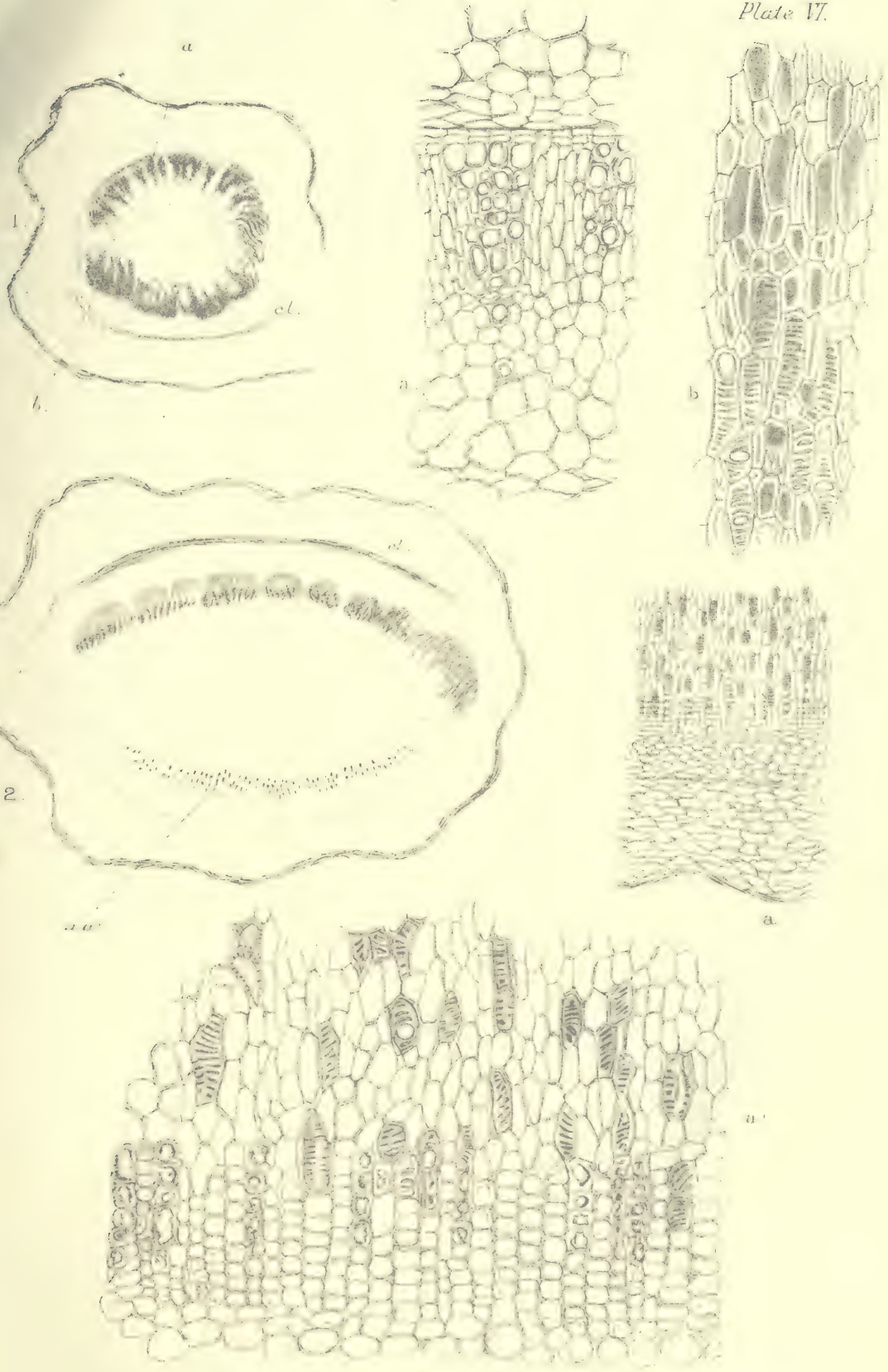

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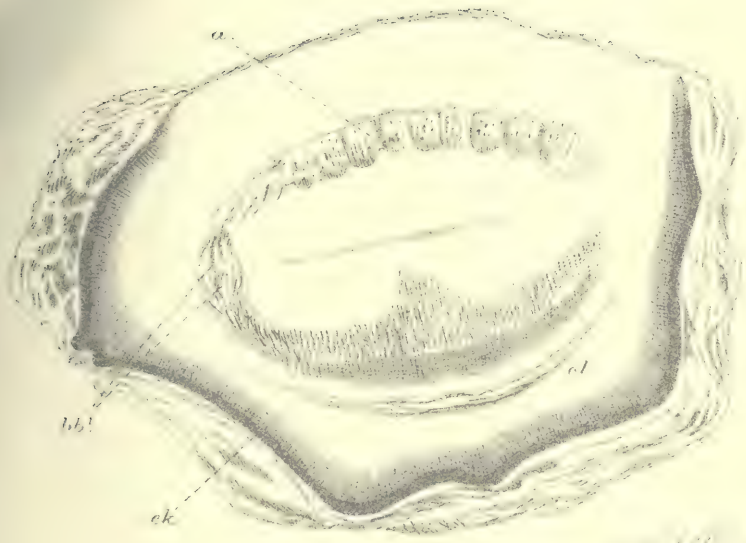
Plate VII.



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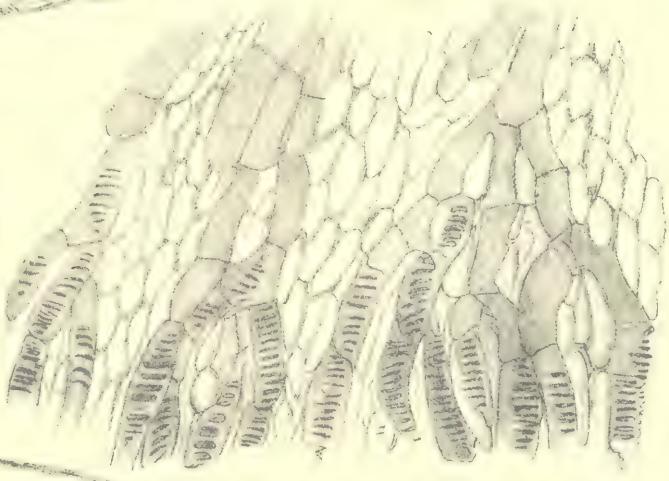

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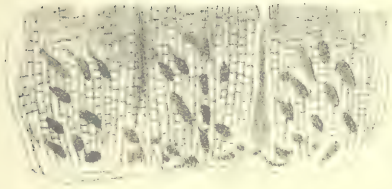

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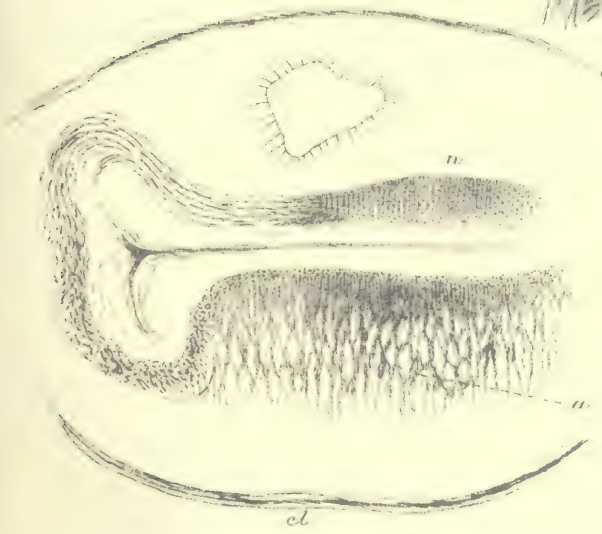

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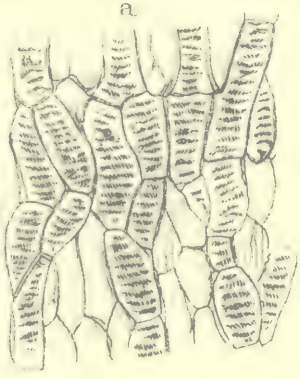

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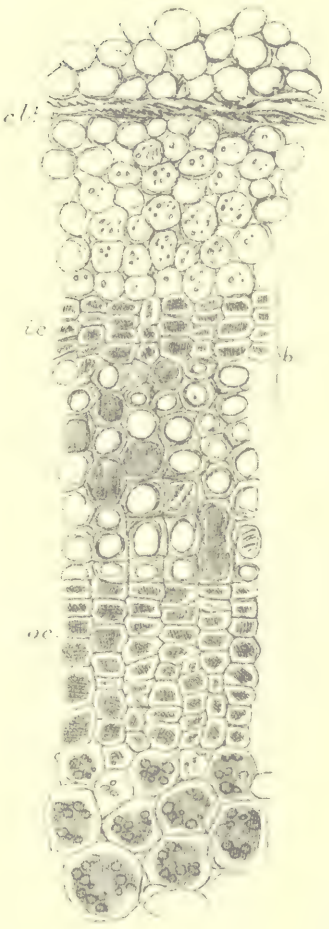
Plate VIII.

a



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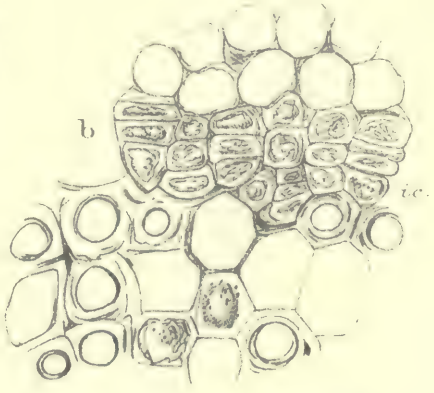
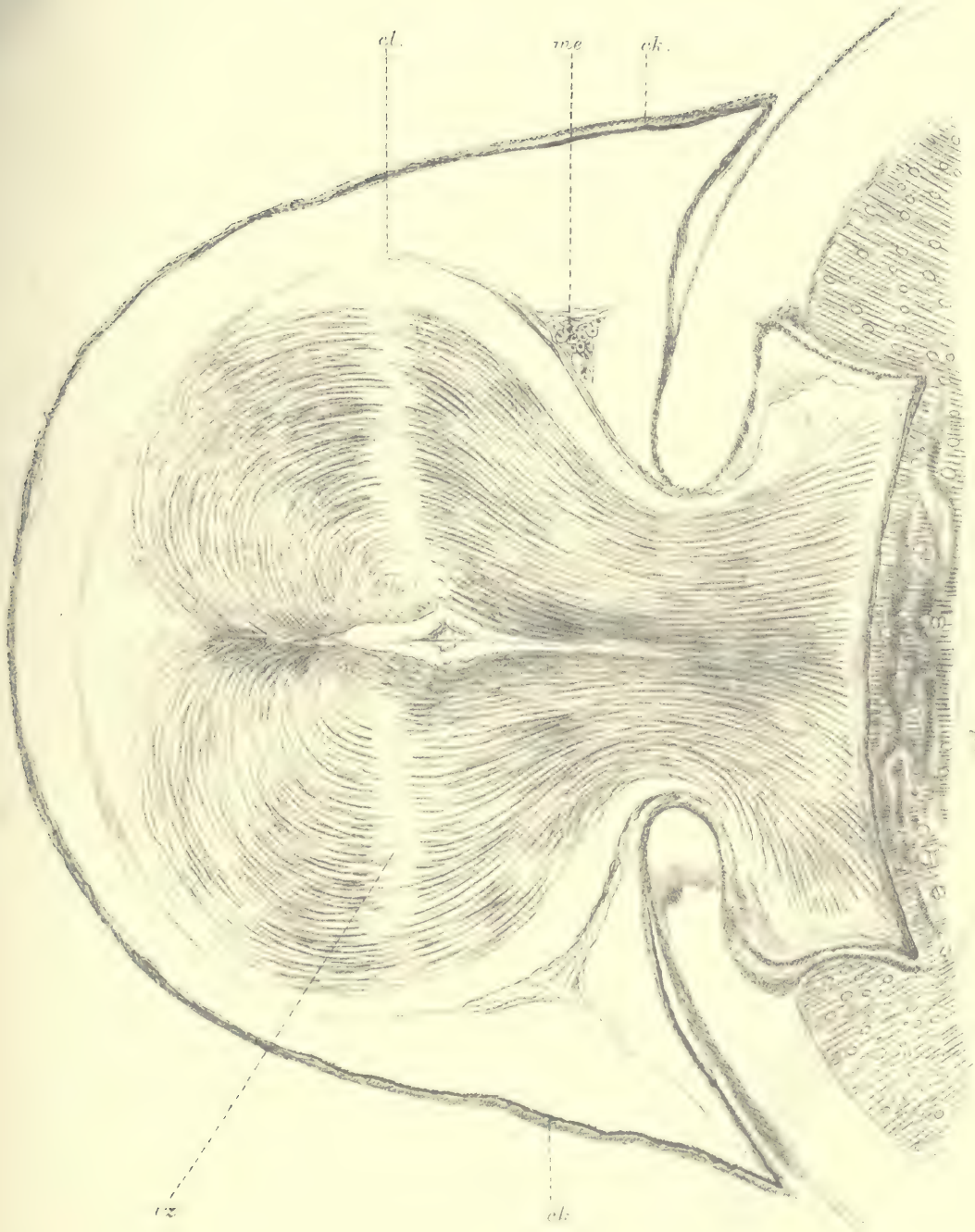


Huth, London.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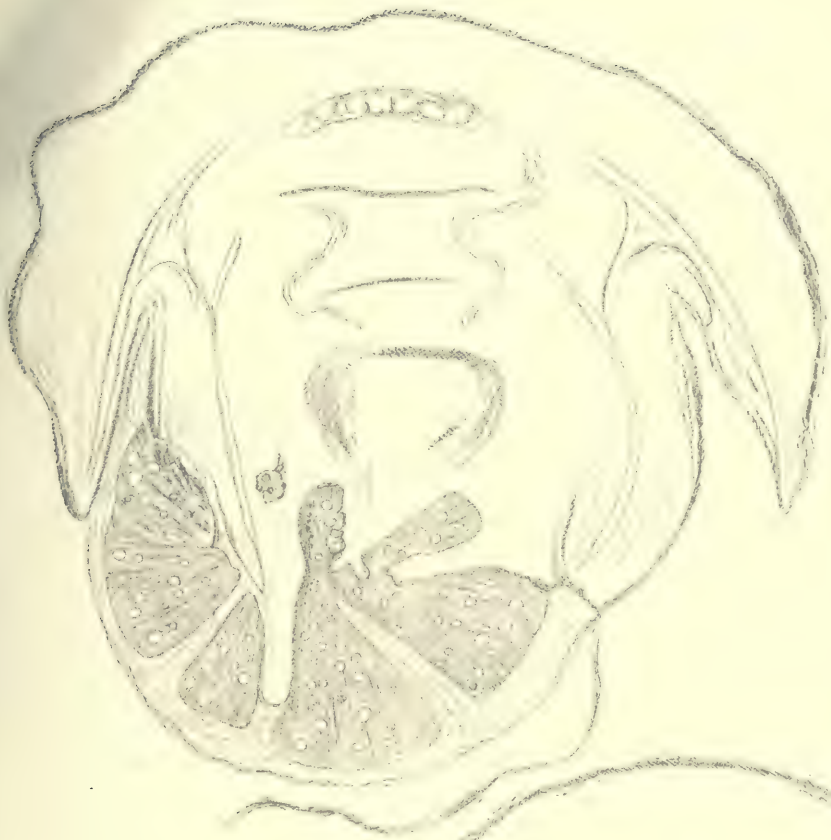

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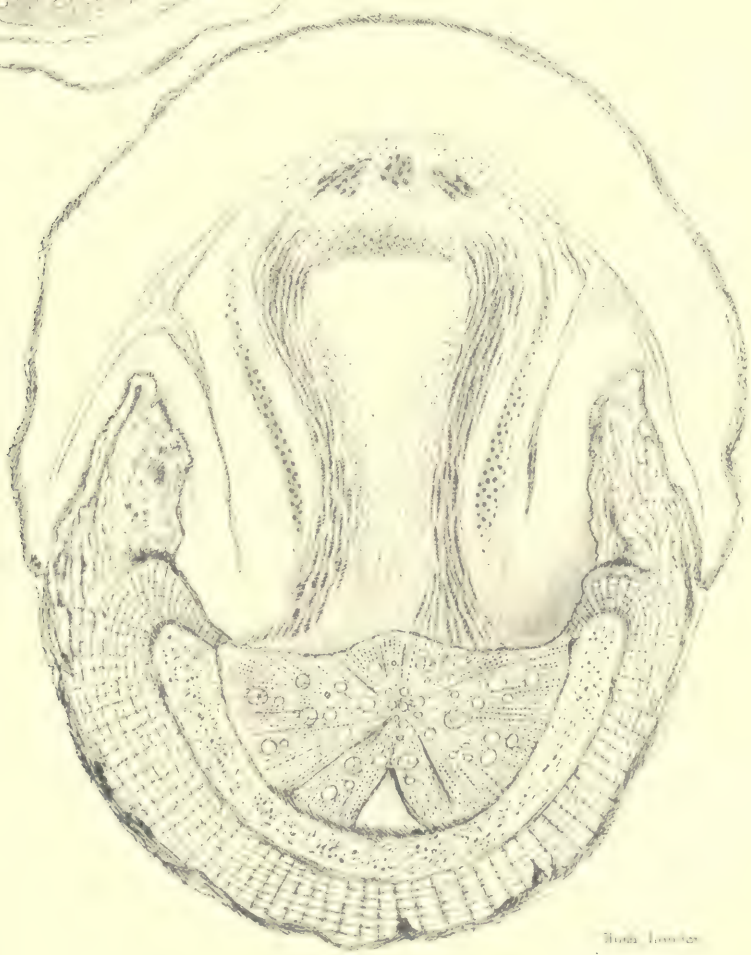

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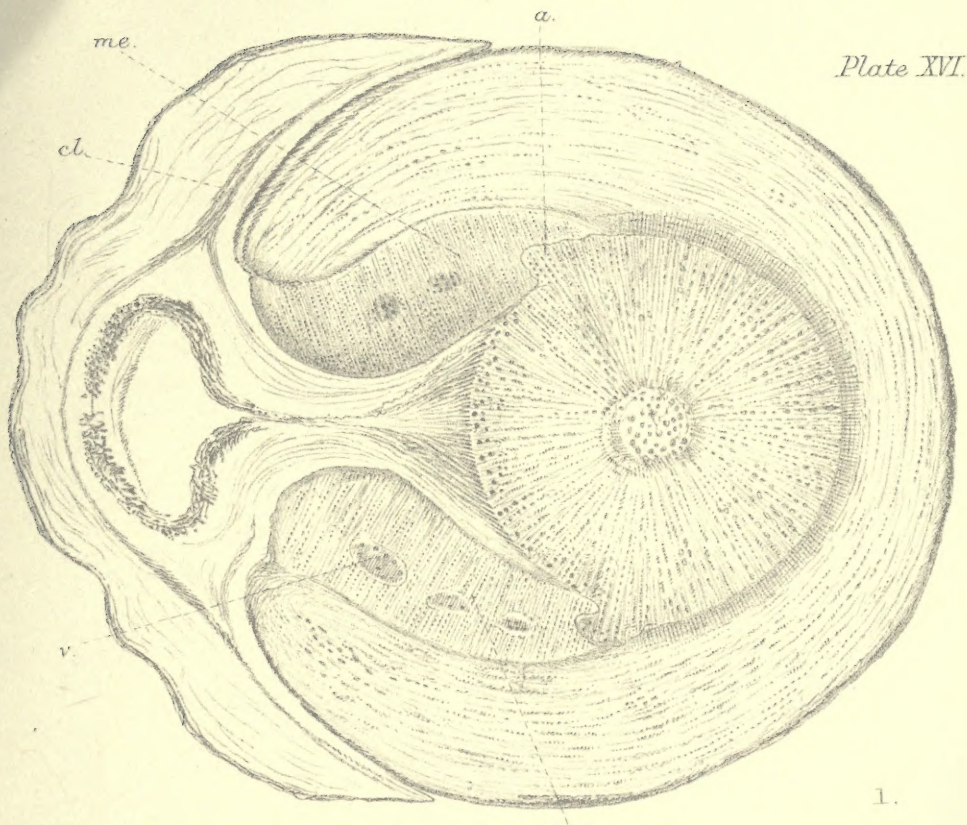
Plate XVI.



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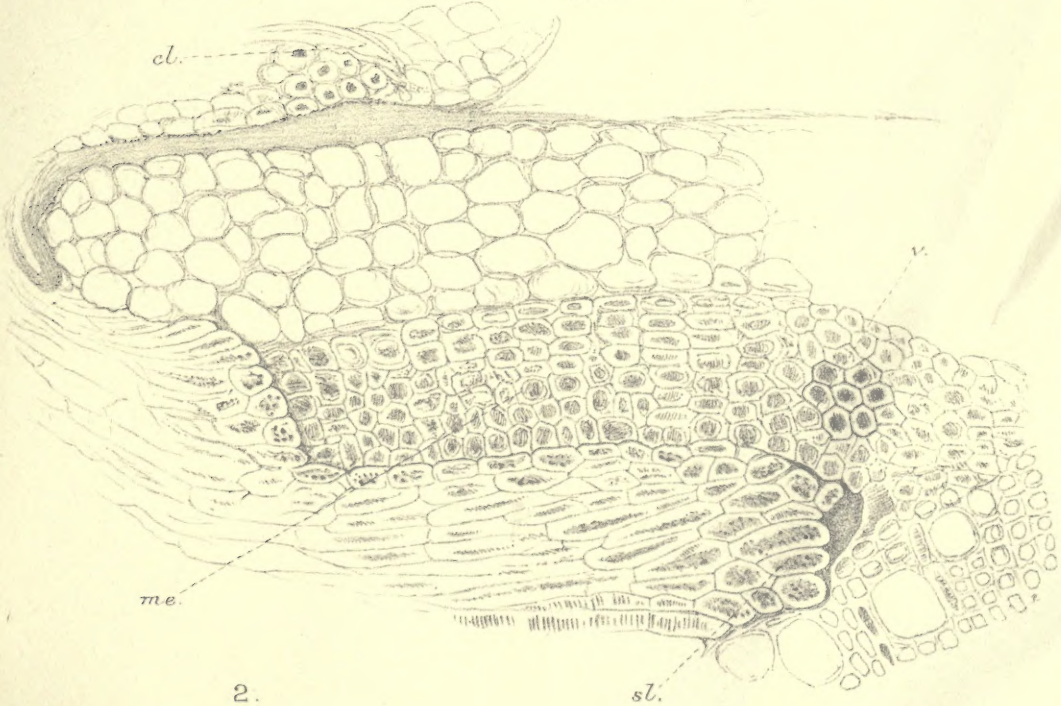

2.

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